Variations in working memory capacity

From cognition to brain networks

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university of groningen

Variations in working memory capacity

From cognition to brain networks

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Dear family, friends, colleagues, reviewers, poster attendants, and interviewers,

I feel

grateful /ˈgreɪt.fəl/ feeling gratitude to someone for a helpful act

thankful /ˈθæŋk.fəl/ glad that something has happened, that someone exists

indebted /ɪnˈdet.ɪd/ owing gratitude to someone because of help given

appreciative /əˈpriː.ʃə.tɪv/ showing an understanding of how good something is

beholden /bɪˈhəʊl.dən/ feeling of having a duty to someone because of what they have done

to every single one of you.

Ačiū.

Table of Contents

1 General Introduction

"Working memory" is the ability to maintain and manipulate information that is no longer available to our senses. We use it when trying to comprehend a story (e.g. linking a pronoun to one of the previously introduced characters), or when following directions of our fellow passenger (e.g., "take the first turn left and then go on a roundabout, third exit"). Minor distractions on the road or thoughts, which are unrelated to the task at hand, sidetrack attention, and the contents of working memory can be lost for good. The above examples indicate that the number of active thoughts kept in our mental cognitive space is limited and vulnerable to distractions. Many studies demonstrate that the "size" of this cognitive space, termed working memory capacity (WMC), varies among healthy people (Redick et al., 2012), is decreased in certain clinical conditions such as Schizophrenia (Johnson et al., 2013), and changes across the lifetime (Cowan, AuBuchon, Gilchrist, Ricker, & Saults, 2011; Park et al., 2002). WMC also fluctuates over shorter periods of time (Klein & Fiss, 1999; Stevens, Tappon, Garg, & Fair, 2012), thus indicating that additional factors such as mental state (e.g. sleep deprivation, mental fatigue) affect our ability to use WM resources (Engle, 2010; Ilkowska & Engle, 2010).

Measures of Working Memory Capacity (WMC)

Measures of WMC are tightly linked to variability in definitions of the term itself (Luck & Vogel, 2013; Shipstead, Redick, Hicks, & Engle, 2012). Some researchers have argued that WMC "is not about the storage or memory per se, but about the capacity for controlled, sustained attention in the face of interference or distraction" (Engle, Kane, & Tuholski, 1999; p. 104), emphasizing the critical role of attention control abilities in defining an individual's WMC. Proponents of this approach use complex span tasks (Figure 1.1A), such as operation span (Unsworth, Heitz, Schrock, & Engle, 2005) and symmetry span tasks (Kane et al., 2004), to estimate WMC. The key component of complex span tasks is the need to switch attention back and forth between the primary memory task (remembering sequences of letters or locations) and the secondary processing task (solving math equations or judging symmetry of complex patterns). As such, complex span tasks resemble real-life situations in which one needs to keep in mind some information while processing other information (e.g. mental two-digit multiplication).

Other researchers suggested that WMC depends on individual differences in the amount of information that can be actively kept in the focus of attention (Cowan et al., 2005; Vogel & Machizawa, 2004). This limited-capacity online workspace was estimated to fit three to five "chunks" of information (Cowan, 2010), and can be measured using a visual change-detection task (Figure 1.1B). In this task, a sample array of colored squares is briefly presented, followed by a blank interval and a test array, which is either different from or identical to the sample array. The task requires detecting changes between sample and test arrays, or localizing the changed item when sample and test arrays are always different (Luck & Vogel, 2013).

Developmental studies (Cowan, Fristoe, Elliott, Brunner, & Saults, 2006; Cowan, Morey, AuBuchon, Zwilling, & Gilchrist, 2010) provided evidence that there are not only individual differences in WM space (storage), but also individuals differ by how efficiently WM space is used to store only relevant information (attention control). Therefore, the use of complex span tasks is arguably a more accurate way of measuring individual's WMC, as it captures both storage and control components, in contrast to the change detection task or simple span tasks (Engle, Tuholski, Laughlin, & Conway, 1999), that capture only storage-related aspect of WMC.

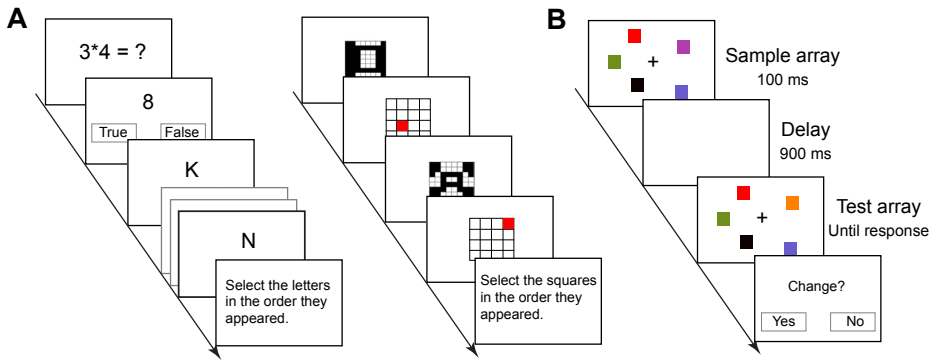

Figure 1.1. Measures of working memory capacity. (A) Examples of trials in the operation and symmetry span tasks (left- and right-side panels, respectively). In complex span tasks, the primary memory task (here, letters or square locations) is interleaved with a secondary processing task (here, solving arithmetic problems or judging the symmetry of figures). Memory items are tested at the end of each list, followed by performance feedback. (B) Example of a single trial in the change-detection task.

Why WMC matters?

On a practical level, WMC (measured using complex span tasks) predict a range of high-level cognitive abilities, such as reading and speech comprehension (Daneman & Carpenter, 1980; Pimperton & Nation, 2012), language learning (Linck, Osthus, Koeth, & Bunting, 2013; Szmalec, Brysbaert, & Duyck, 2012), scholastic achievement (Alloway, 2009; Daneman & Carpenter, 1980), and novel problem solving (Engle, Tuholski et al., 1999; Kane et al., 2004). Therefore, for example, remembering that some of the audience members may have low-WMC can be helpful when organizing a lecture. Grouping information, linking facts together, and reminding what was previously said will help the audience better understand and remember the lecture (Stafford & Webb, 2005).

An individual's WMC predicts not only high-level cognitive functioning, but also performance in rather simple tasks that require control of attention and have minimal memory demands (Engle & Kane, 2004). For example, WMC-related differences are found in interference tasks, in which conflicts have to be resolved between habitual stimulus-response associations and those required by the task. In the anti-saccade task (Kane, Bleckley, Conway, & Engle, 2001; Unsworth, Schrock, & Engle, 2004), for example, it is more difficult to follow task instructions to look away from a flash of light (make an anti-saccade) than to look towards the flash of light (make a pro-saccade). Low- compared to high-WMC individuals are slower and more error-prone when responding on antisaccade trials (Kane et al., 2001; Unsworth et al., 2004). Differences in the ability to maintain a task goal (e.g., look away from the light) due to episodes of mind-wandering and occasional forgetting of the task goal (i.e., "attentional failures") are thought to be the primary reason for individual differences in WMC-related sensitivity to the distracting information (Unsworth et al., 2004).

Internal (e.g. mind-wandering) or external (e.g. sudden loud noise or bright light) attentional failures might have serious real-world consequences. Fluctuations in attentional state can explain why the experience of "not seeing" another car and hitting the brakes just in time (or too late) is as common as it is: Brief attentional lapses may prolong visual-processing time (e.g., seeing another car) and result in the delayed initiation of action (Johnson & Gulbinaite, 2013).

Executive-attention theory of WMC

Engle and colleagues summarized a wealth of evidence from numerous correlational and latent-variable analysis studies and formulated the *executive-attention theory* of WMC (Engle & Kane, 2004; Kane, Conway, Hambrick, & Engle, 2007). According to this theory, co-variation between performance in complex span tasks and general cognitive abilities stems from variation in control of attention in the face of distraction (executive attention). Furthermore, Kane and Engle distinguished two aspects of executive attention that are related to variations in WMC: Active maintenance of task goals and resolution of response conflict.

WMC-related differences in interference tasks have been most consistently reported in task contexts in which 70%-80% of trials were congruent (Kane & Engle, 2003; Long & Prat, 2002; Morey et al., 2012; Unsworth, Redick, Spillers, & Brewer, 2011; see Table 1.1). Frequent congruent trials challenge goal-maintenance abilities, because the likelihood of actively maintaining task goals is decreased when habitual stimulus-response associations are correct on a majority of trials (e.g., in the Stroop task when the word meaning and color match). Low- compared to high-WMC individuals are slower to respond and make more errors on infrequent incongruent trials. This finding supports the idea that individual differences in WMC reflect differences in the ability to keep task goals active when task context does not support it (Braver, Gray, & Burgess, 2007; Kane et al., 2007).

The evidence that individual differences in WMC and performance in conflict tasks with which they correlate not only reflect goal-maintenance abilities, but also variations in conflict processing is mixed (see Table 1.1). Following the reasoning of Kane and Engle (2003), task contexts with a high proportion of incongruent trials should facilitate goal maintenance and highlight WMC-related differences in conflict processing. Group differences in the size of interference effects (the performance difference between incongruent and congruent trials) were rarely found when task goals were supported contextually by increasing the proportion of incongruent trials up to 50% (Heitz & Engle, 2007; Keye, Wilhelm, Oberauer, & Sturmer, 2013; Keye, Wilhelm, Oberauer, & van Ravenzwaaij, 2009; Wilhelm, Hildebrandt, & Oberauer, 2013), or even 70% or 80% (Meier & Kane, 2012; Morey et al., 2012; Weldon, Mushlin, Kim, & Sohn, 2013; see Table 1.1). This raises the question whether WMC-related differences in interference effects can be explained by variability in how cognitive control is adjusted in response to conflict, or whether high- and low-WMC individuals differ only in the ability to maintain task goals (Unsworth et al., 2011).

Although the executive-attention theory does not make specific predictions about WMC-related differences in trial-to-trial adjustments in cognitive control in response to conflict, the size of interference effects depends on the previous trial context (congruency sequence effects, CSEs; Egner, 2007). Following the executive-attention theory of WMC, one could expect that the ability of high-WMC individuals to resolve conflict faster would also allow them to exert control more effectively on the next trial, thus showing a positive relationship between WMC and the size of CSEs (Keye et al., 2009). On the other hand, a better ability of high- compared to low-WMC individuals to maintain task goals would suggest that they are less affected by interference from task-irrelevant information in the first place, and thus a negative relationship between WMC and CSEs could be expected (Meier & Kane, 2012). Although the latter alternative received some support (Hutchison, 2011; Keye et al., 2009), the relationship between WMC and CSEs is not always found (see Table 1.1).

The evidence for WMC-related differences in the size of interference effects and CSEs

shows little agreement across three commonly used interference tasks (Simon, Eriksen flankers, and Stroop). The meta-analysis of 13 studies (26 experiments) reported in the Table 1.1 shows that WMC-related differences are mostly found in predominantly congruent-trial task contexts, and the effect of WMC on the size of CSEs is found only in variants of the Simon and Stroop tasks, but not in the Eriksen flanker task. These inconsistent results clearly indicate the need to explore the boundary conditions of the relationship between WMC and cognitive control.

The behavioral study described in Chapter 2 of this thesis was designed to test whether the often-observed differences in interference task performance reflect WMC-related differences in conflict processing, and are not only related to variations in goal maintenance abilities (Morey et al., 2012; Unsworth et al., 2011). To get more insight into WMC-related differences in the dynamics of conflict resolution we examined the entire RT distribution using delta plots (Proctor, Miles, & Baroni, 2011). The results of the study supported the idea that WMC-related differences in interference task performance reflect variations in conflict processing, and also revealed WMC-related differences in cognitive control adjustments to the previous trial conflict.

Neural mechanisms responsible for differences in WMC

There is ample evidence that individuals scoring relatively low on WMC measures demonstrate increased sensitivity to auditory and visual distractions (Brumback, Low, Gratton, & Fabiani, 2004; Kane et al., 2007; Sorqvist, 2010). For example, they more often than high-WMC individuals notice salient stimuli such as their own name in the dichotic listening task (Conway, Cowan, & Bunting, 2001), or are slower to focus attention to the relevant stimuli in the Eriksen flanker task (Heitz & Engle, 2007). These findings would suggest that high-WMC individuals compared to low-WMC ones are more apt to suppress, or filter out, various sources of distraction. However, ability to focus on relevant information, or selective attention, depends on two mechanisms: Suppression of irrelevant information and enhancement of relevant information (Corbetta & Shulman, 2002). It is unknown whether WMC-related differences in selective attention reflect differences in suppression of irrelevant information (Hasher, Lustig, & Zacks, 2007), or enhancement of relevant information (Heitz & Engle, 2007), or a combination of both.

Indirect evidence for WMC-related differences in suppression of irrelevant information is provided by a cognitive aging study that measured changes in early event-related potentials, the P1/N1 complex (Gazzaley et al., 2008). Typically, the amplitude of P1/N1 complex is increased to the attended stimuli, whereas it is decreased for the unattended stimuli, compared to passive viewing conditions (e.g. Gazzaley et al., 2005). Gazzaley and colleagues (2008) demonstrated age-related impairments in suppressing irrelevant information with no or weak changes in enhancement of relevant information. Moreover, they found that decreased ability to suppress irrelevant information was reflected in impaired WM task performance, as the limited capacity WM system was filled with task-irrelevant rather than task-relevant information. Although these findings may seem to imply that variations in WMC might be related to differences in suppression of irrelevant information, cognitive aging involves multifaceted changes in the brain that are not limited to the working memory system. Moreover, even this indirect evidence is compromised by the fact that attention-related changes in P1/N1 amplitude cannot be attributed unequivocally to enhancement of attended stimuli or suppression of unattended stimuli, and most likely reflect both processes (Couperus & Mangun, 2012). This leaves the question about the neural mechanisms related to WMC still open.

Table 1.1. The relationship between WMC (as measured by complex span tasks) and cognitive control abilities, operationalized as the size of interference effects and congruency sequence effects (CSEs).

Study	Experimental Paradigm (ratio congruent/incongruent trials)	Effect of WMC on interference effects	Effect of WMC on CSEs
Long & Prat (2002)	Stroop (-/20) [1] Stroop (-/80) [1]	+ -	N/A
Kane & Engle (2003, Exp 4)	Stroop (80/20) Stroop (20/80)	+ +	N/A
Kiefer et al. (2005)	Stroop (33/33) [2]	+	N/A
Heitz & Enlge (2007)	Eriksen flanker (50/50)	-	N/A
Keye et al. (2009)*	Vertical Simon (50/50) Eriksen Flanker (50/50)	- -	+ -
Unsworth et al. (2011)	Stroop (67/33) Eriksen Flanker (33/33) [2]	+ +	- -
Hutchison (2011)	Stroop (67/33) Stroop (33/67)	+ -	+ +
Shipstead & Broadway (2012)	Stroop (43/43) [3]	+	N/A
Morey et al. (2012)	Stroop (-/82) [4] Stroop (60/20) [4]	- +	N/A
Meier & Kane (2013)	Stroop (70/30) [5] Stroop (30/70) [5] Stroop (70/30) [6]	- + +	- - -
Weldon et al. (2013)	Horizontal Simon (50/50) Horizontal Simon (80/20) Horizontal Simon (20/80)	- - -	+ - -
Wilhelm et al (2013)*	Vertical Simon (50/50) Eriksen Flanker (50/50)	- -	N/A
Keye et al. (2013)*	Simon (50/50) [7] Simon (80/20) [7] Simon (20/80) [7]	- - -	- - -

Notes: The table includes only studies in which healthy young participants were tested. Plus signs indicate studies, in which high-WMC was associated with smaller interference effects and smaller congruency sequence effects. Minus signs indicate studies, in which no WMC-related differences were found. N/A stands for "non-applicable", indicating that the effect was not reported.

* Structural equation modeling analysis techniques were used, other studies used mixed ANOVAs.
[1] Neutral instead of congruent trials were presented.
[2] Neutral trials comprised 33% of all trials.
[3] Neutral trials comprised 14% of all trials.
[4] Exp1: Congruent (9%) and non-color word trials (9%). Exp2: 20% of all trials were neutral.
[5] Six-color Stroop task was used.
[6] Three-color Stroop task was used.
[7] Horizontal and Vertical Simon tasks were used.

The study documented in Chapter 3 was therefore designed to test *directly* whether WMC-related differences in attentional control are mediated by a stronger enhancement of relevant sensory information, suppression of irrelevant sensory information, or a combination of both. An approach that allowed us to track attention allocation to each of several simultaneously presented stimuli is called "frequency tagging". The method is based on rhythmic visual (or auditory) stimulation, which elicits steady-state visual evoked potentials (SSVEPs). The SSVEP is a rhythmic response observed in EEG at the frequency that corresponds that of the rhythmic stimulation (Regan, 1977). Most importantly, SSVEP amplitude is modulated by the amount of attention paid to the stimuli, with the amplitude of SSVEP enhanced when an object or a specific feature is attended, and suppressed when it is unattended (Andersen & Muller, 2010; Muller, Malinowski, Gruber, & Hillyard, 2003).

To investigate WMC-related differences in suppression of irrelevant information and enhancement of relevant information, the Eriksen flanker paradigm was chosen (Eriksen & Eriksen, 1974). In this paradigm, task-relevant (target) and task-irrelevant (flankers) stimuli are presented simultaneously, and thus mimic everyday visual experiences when multiple objects compete for attention. By tagging the target and flankers with different frequencies and measuring steady-state visual evoked potentials (SSVEPs) we were able to dissociate the processing of relevant and irrelevant information and compare it between high- and low-WMC individuals. The results indicated that low-WMC individuals indeed failed to suppress distractors, however they did enhance the targets (the opposite pattern was found for the high-WMC participants), resulting in similar performance as compared to the high-WMC group.

Neural correlates of relationship between WMC and cognitive control

Recent meta-analyses of neuroimaging studies have consistently found the same brain network to be active in working memory and cognitive control tasks (e.g., the N-back and Stroop tasks), a common feature of which is a need to keep task goals active in the face of interference (Burgess, Gray, Conway, & Braver, 2011; Nee, Wager, & Jonides, 2007; Niendam et al., 2012). The network is generally referred to as the "cognitive control network" (Cole & Schneider, 2007), which among other areas includes dorsolateral prefrontal cortex (DLPFC), medial frontal cortex (MFC) and parietal regions. DLPFC is proposed to be involved in the representation and maintenance of task goals—as well as in the implementation of cognitive control—by suppressing task-irrelevant information (Miller & Cohen, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004) and the MFC is suggested to be involved in detecting conditions in which increased cognitive control is required (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004). More importantly, recent reports emphasize that connectivity between DLPFC and other parts of the cognitive control network might be relevant for individual differences in both WMC and cognitive control abilities (Cole, Yarkoni, Repovs, Anticevic, & Braver, 2012; Edin et al., 2009; Faraco et al., 2011).

Although fMRI studies revealed the brain networks involved in WM and cognitive control, the exact role that each area plays in such a complicated system and how the temporal dynamics of these networks relate to individual differences in WMC is currently unknown. Changes in functional connectivity at behaviorally relevant timescales might be missed by

fMRI, and cannot be measured with event-related potentials (Cohen, 2011b).

The frequently observed relationship between WMC and performance in attentional control tasks could result from reduced processing of distracting information at an early stimulus-processing stage, but may also result from differences at a later, response-selection stage. For example, several studies suggested that high WMC individuals are capable of responding faster through suppression of distracting information early in the processing. Long and Prat (2002) favored this explanation because of the stronger negative priming effects (slower responses on trials in which hue matches the Stroop-word of the previous trial) in the high- as compared to the low-WMC group. Similarly, Fukuda and Vogel (2009) demonstrated that high-WMC participants were able to fixate on the task-relevant object and to resist attentional capture by suddenly presented task-irrelevant objects, whereas low-WMC individuals were less capable of doing so. Although this supports an early locus of WMC differences in attention control, WMC-related differences in the later stages of stimulus processing are unexplored.

In the Chapter 4 of this thesis we sought to characterize WMC-related differences in large-scale network dynamics related to conflict processing and trial-to-trial adjustments in response to the previous trial conflict signal. For this purpose we recorded EEG while subjects performed a Simon task and used time-frequency analysis tools for data analysis. The results of this study suggest that the relationship between WMC and cognitive control abilities is more strongly reflected in large-scale oscillatory network dynamics in theta and delta frequency bands than in spatially localized activity or in behavioral task performance.

Outline of the thesis

The study documented in Chapter 2 tests the prediction suggested by executive-attention theory of WMC (Kane & Engle, 2003) that WMC-related differences in interference effects are related to variations in the proficiency of conflict resolution and not only to variability in goal-maintenance abilities. By manipulating the difficulty of trial-by-trial conflict resolution in the Simon task and employing RT distribution analyses, we demonstrated that there are WMC-related differences in the time course of conflict processing, especially under the difficult task condition. We hypothesized that such results can be explained by the ability of high-WMC individuals to employ a proactive control strategy when the need for control is high, whereas low-WMC individuals rely more on a reactive control strategy.

The study described in Chapter 3 focused on whether frequently observed WMC-related differences in attentional control reflect differences in the ability to suppress task-irrelevant information, or enhance task-relevant information. For this purpose, a novel experimental approach was used that allowed us to track simultaneously the attention to relevant and irrelevant information in a modified Eriksen flanker task using the EEG frequency tagging technique. The results of this study reveal that high and low WMC individuals use different strategies to achieve similar performance: High-WMC individuals focus on suppressing irrelevant information, whereas low-WMC individuals focus on enhancing relevant information.

The study documented in Chapter 4 aimed to characterize ways in which large-scale network functioning as measured with EEG may differ between high- and low-WMC individuals during conflict processing and adaptation to conflict. The findings of this study revealed that although high- and low-WMC individuals did not differ behaviorally, there were substantial WMC-related differences in theta- (4-8 Hz) and delta-band (1-3 Hz) connectivity in a fronto-parietal network. These findings suggest an explanation for the weak relationship between WMC and behavioral performance in interference tasks and reveals that WMC-related differences in cognitive control abilities are more subtle than the executive-attention theory predicts, and that measures more sensitive than RT and error rates are required to uncover this relationship.

Chapter 5 of this thesis is an opinion paper that discusses five methodological challenges in current cognitive electrophysiology literature, with a particular focus on the roles of brain oscillations in cognition. In the context of Chapters 2-4 of this thesis, the most relevant among the five challenges is “Challenge 5: Developing neurophysiologically grounded psychological theories”, which discusses the need to update existing cognitive models with neurophysiological findings to make more specific predictions that could speed-up the progress in understanding neurophysiological bases of cognition.

Chapter 6 concludes the thesis with an integrated overview of the current work, and suggests possible directions for the future research.

2 Behavioral evidence for the relationship between WMC and Cognitive Control

The relationship between the ability to maintain task goals and working memory capacity (WMC) is firmly established, but evidence for WMC-related differences in conflict processing is mixed. We investigated whether WMC (measured using two complex-span tasks) mediates differences in adjustments of cognitive control in response to conflict. Participants performed a Simon task in which congruent and incongruent trials were equiprobable, but in which the proportion of congruency repetitions (congruent trials followed by congruent trials or incongruent trials followed by incongruent trials) and thus the need for trial-by-trial adjustments in cognitive control varied by block. The overall Simon effect did not depend on WMC capacity. However, for the low-WMC participants the Simon effect decreased as the proportion of congruency repetitions decreased, whereas for the high- and average-WMC participants it was relatively constant across conditions. Distribution analysis of the Simon effect showed more evidence for the inhibition of stimulus location in the low- than the high-WMC participants, especially when the proportion of congruency repetitions was low. We hypothesize that low-WMC individuals exhibit more interference from task-irrelevant information due to weaker preparatory control prior to stimulus presentation and, thus, stronger reliance on reactive recruitment of cognitive control.

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Introduction

Most everyday actions are performed in a more or less automatic manner, making performance fast and efficient. However, when confronted with novel or ambiguous situations in which several conflicting action alternatives are possible, it is necessary to exercise cognitive control to achieve accurate performance. Recruitment of cognitive control can be reactive, in the sense that it is triggered by the environment, or proactive, in the sense that control strategies are adopted in advance to cope with the demands of a specific situation (Braver, 2012).

Cognitive control processes are usually studied using so-called conflict tasks (for a review, see Egner, 2007). In such tasks, overlap between stimulus and/or response dimensions gives rise to conflicting response tendencies (Kornblum, Hasbroucq, & Osman, 1990). In a typical version of the Simon task (Simon, 1969), for example, each stimulus is characterized by two dimensions: A relevant dimension (e.g., stimulus shape) assigned to left- and right-side keypresses and an irrelevant dimension (stimulus location). On *congruent* trials, the relevant and irrelevant stimulus dimensions are both associated with the same response (e.g., a left-side keypress to a stimulus presented on the left), whereas on *incongruent* trials they are associated with conflicting responses (e.g., a right-side keypress to a stimulus presented on the left). The need to resolve response conflict on incongruent trials typically results in longer reaction times (RTs) and higher error rates than on congruent trials. This difference in RT and error rates for congruent and incongruent trials is generally termed an *interference effect*.

Successful performance in conflict tasks requires active maintenance of task goals (i.e., stimulus-response mappings) in working memory and recruitment of cognitive control to resolve conflict between habitual stimulus-response associations and those required to meet task goals. Kane and Engle (2003) have suggested that both the ability to maintain task goals and the speed of conflict resolution are related to variations in working memory capacity (WMC) as measured by complex span tasks (e.g., the Operation span task; Unsworth et al., 2005). Kane and Engle showed that high-WMC individuals are less susceptible to interference from the task-irrelevant stimulus dimension in a colour-word Stroop task (MacLeod, 1991) in that they are better able to keep the task goal (ignore the word meaning) active even when the proportion of congruent trials is high (80%). Moreover, they showed that differences in the size of interference effects between high- and low-WMC groups persisted even under conditions in which the task environment should have supported the goal of responding to the relevant stimulus dimension and suppressing responses to the irrelevant dimension (i.e., when the proportion of incongruent trials was 80%).

WMC-related differences in cognitive control have been most consistently observed in task contexts that feature predominantly congruent trials (Kane & Engle, 2003; Long & Prat, 2002; Morey et al., 2012; Unsworth et al., 2011). This finding lends support to the idea that individual differences in WMC and the performance in conflict tasks with which they correlate reflect differences in the ability to keep task goals active when the task environment does not support goal maintenance (Braver et al., 2007; Kane et al., 2007). However, the idea that high-WMC individuals are faster in resolving conflict between automatically elicited and required responses within a given trial — as also suggested by Kane and Engle (2003) — has not received overwhelming support. Differences between high- and low-WMC groups in interference effects have not generally been found in studies in which the task goal was supported contextually by presenting equal numbers of congruent and incongruent trials (Heitz & Engle, 2007; Keye et al., 2009; Weldon et al., 2013), or predom-

inantly incongruent trials (Weldon et al., 2013). These findings throw into question whether overall WMC-related differences in RTs and accuracy can be explained by variability in how cognitive control is adjusted in response to conflict, or whether WMC-related individual differences reflect only differences in the ability to maintain goals (Unsworth et al., 2011).

The overall differences in the size of interference effects between groups reflect a cumulative effect of trial-to-trial adjustments in cognitive control, thus examining sequence effects in conflict tasks can provide more insight into WMC-related differences in conflict resolution. Typically, the interference effect is smaller following incongruent trials than following congruent ones (Gratton, Coles, & Donchin, 1992; Kerns et al., 2004; Sturmer, Leuthold, Soetens, Schroter, & Sommer, 2002). Such *congruency sequence effects* (CSEs) have been interpreted in terms of dynamic trial-to-trial changes in cognitive control in response to conflict. According to *conflict monitoring theory* (Botvinick et al., 2001), cognitive control is relaxed following congruent trials, during which processing can be relatively automatic, and proactively engaged following incongruent trials. Thus, on post-incongruent trials (*iI* and *iC* trials) the influence of task-irrelevant information is reduced prior to stimulus presentation by proactive recruitment of cognitive control processes (Botvinick et al., 2001; Braver et al., 2007; Ullsperger & King, 2010). Such post-conflict increase in cognitive control diminishes automatic response capture on iI trials, however, it also decreases any facilitative effect of task-irrelevant information on iC trials, resulting in reduced interference effects relative to trials preceded by congruent trials (*cC* and *cI* trials), for which, presumably, control is not proactively engaged.

In contrast to accounts of CSEs that emphasize top-down changes in cognitive control (Botvinick et al., 2001), the feature integration account (Hommel, Proctor, & Vu, 2004) emphasizes the importance of bottom-up effects (for a review, see Egner, 2007). According to this account, stimulus features and responses are automatically bound into an episodic memory representation (an event file) on every trial, and repetition of any of the features from the previous trial triggers the automatic retrieval of the entire event file from the previous trial. Whereas feature binding is assumed to be automatic, unbinding is assumed to require cognitive control. Thus, responses on trials in which all features (complete repetition trials) or no features (complete alternation trials) are repeated from the previous trial will be faster than partial repetitions for which some features must be unbound from the previous event file. In two-alternative Simon task in which one of two imperative stimuli is shown on each trial in a position that is either spatially congruent or incongruent with the response, congruency repetitions are confounded with stimulus and/or response repetitions and alternations. On cC and iI trials, either both stimulus and response are repeated or neither stimulus nor response is repeated, which facilitates responding because no unbinding is required. On iC and cI trials, stimulus-response pairs always involve partial repetitions (i.e. either stimulus or the location of the stimulus is repeated) and are thus subject to unbinding costs. In short, although different accounts of CSEs are not mutually exclusive (for a review, see Egner, 2007; Notebaert, Gevers, Verbruggen, & Liefooghe, 2006) and differ in the mechanisms they propose, they share the idea that changes in cognitive control underlie CSEs. Control is required for unbinding in the feature-integration account (Hommel et al., 2004) or for reducing the influence of task-irrelevant features in the upcoming trial in conflict monitoring theory (Botvinick et al., 2001; cf. Spape, Band, & Hommel, 2011).

Following the reasoning of Kane and Engle (2003), high- and low-WMC individuals should differ in CSEs. If high-WMC individuals are faster at resolving conflict on the current

trial, they should also more effectively exert control on the following trial, thus showing bigger CSEs than low-WMC individuals. Alternatively, if high-WMC individuals are better than their low-WMC counterparts at maintaining appropriate task goals they should be less affected by interference from task-irrelevant information and thus show smaller CSEs (Meier & Kane, 2012). Support for the latter alternative has been found using a Simon task. A small negative correlation (-.22) between WMC and CSEs has been found in a vertical version of the Simon task (N = 148). More recently, Weldon et al. (2012) using a horizontal version of the Simon task showed that WMC-related differences in CSEs are driven by differences in the size of the Simon effect both on post-congruent and also on post-incongruent trials. That is, low-WMC individuals show both a bigger Simon effect after congruent trials and a bigger reverse Simon effect after incongruent trials as compared to high-WMC individuals (N = 122). In other conflict tasks, such as an Eriksen flanker task or a colour-word Stroop task, WMC-related differences in CSEs are not typically found (Keye et al., 2009; Meier & Kane, 2012; Unsworth et al., 2011; Wilhelm et al., 2013).

One possible explanation for the lack of consistency in the relation between WMC and interference effects and CSEs rests in the data analysis methods used. Relying only on mean RTs may have concealed important differences in the time course of conflict processing between high- and low-WMC groups. An examination of the entire distribution of RTs might provide more insight into differences in the dynamics of conflict processing and trial-to-trial adjustments in cognitive control. RT distribution analysis using delta-plots (in which the interference effect for RTs is plotted as a function of response time) have been shown to reflect the within-trial development of active suppression of incorrect responses, or reactive control (Ridderinkhof, 2002a, 2002b; Wylie, Ridderinkhof, Bashore, & van den Wildenberg, 2010). Because the recruitment of reactive control takes time, the effects of such control on performance are most evident when RTs are slow. In fact, the positive Simon effect seen when responses are fast is often eliminated or even reversed when responses are slow (De Jong, Liang, & Lauber, 1994; for a review, see Proctor et al., 2011). Therefore, the degree to which interference effects are reduced in the slowest portion of the delta-plot is thought to reflect the strength of reactive control.

The need to engage in reactive conflict resolution depends on whether or not control is engaged proactively prior to stimulus presentation. If proactive control mechanisms are in place, the influence of task-irrelevant information will be reduced and there will be less need to resolve conflict reactively, resulting in a less negative delta-plot slope (Ridderinkhof, 2002a, 2002b; Winkel et al., 2011). The effects of proactive control are evident not only in the final slope of RT delta-plots, but also in accuracy delta-plots and conditional accuracy functions (Ridderinkhof, 2002). For example, a transient increase in proactive control in post-incongruent trials as compared to post-congruent trials is marked by a smaller number of fast errors and smaller interference effects at the fastest quantile of delta-plots of accuracy data (Wylie, Ridderinkhof, Bashore, & van den Wildenberg, 2010).

According to Braver and colleagues (Braver, 2012; Braver et al., 2007), maintaining high levels of proactive control is metabolically demanding and the utility of such a strategy will therefore depend on the task context and the ability of the performer. Burgess and Braver (2010), using the "recent negatives" task–a task which requires the resolution of interference between relevant and irrelevant memory traces—demonstrated that proactive control was more likely to be exercised by those high in fluid intelligence, a measure that is highly correlated with WMC when short-term memory span is partialled out (Conway, Cowan,

Bunting, Therriault, & Minkoff, 2002). Burgess and Braver hypothesized that reactive control is a default mode of control because such control is sufficient to resolve occasionally occurring conflict. Proactive control, on the other hand, is resource-demanding and only individuals possessing sufficient cognitive resources, such as high-WMC individuals, are likely to engage in proactive control and only in task contexts that might benefit from such a strategy. Evidence for individual differences in preference for proactive or reactive conflict resolution has also been shown using a Simon task. Individual differences in reactive control as measured by the steepness of the slowest portion of the delta-plot have been found to covary with the strength of activations in brain areas involved in response inhibition (Forstmann, Jahfari et al., 2008; Forstmann, van den Wildenberg, & Ridderinkhof, 2008). Taken together, these findings suggest that reliance on reactive or proactive control processes in conflict resolution may depend on characteristics of an individual.

The present study was designed to investigate WMC-related differences in conflict processing by having participants relatively high or low in WMC as measured with two complex-span tasks (Operation and Symmetry span) perform a Simon task under conditions that varied in difficulty of trial-by-trial conflict resolution. Equal percentages of congruent and incongruent trials were presented in each condition to encourage the maintenance of the task goal and thus isolate — following the reasoning of Kane and colleagues (Engle & Kane, 2004; Kane et al., 2007; Kane & Engle, 2003) — WMC-related differences in conflict processing. We manipulated across conditions the ratio of congruency repetitions (i.e., cC and iI trials) vs. alternations (i.e., cI and iC trials). Congruency alternations are associated with stronger response-selection conflict and thus require more cognitive control than congruency repetitions (Hommel et al., 2004). By changing the proportion of congruency alternation trials, we created three task contexts in which the need for trial-to-trial adjustments was high (25% congruency repetitions), medium (50% congruency repetitions), or low (75% congruency repetitions). A similar manipulation in a Stroop task has been shown to slow down RTs when the proportion of congruency repetitions was low (30%) as compared to when it was high (70%; Jimenez & Mendez, 2013).

To test whether individuals scoring high and low in WMC differ in their preference for reactive or proactive conflict resolution, we compared the time-course of conflict resolution across conditions using a delta-plot approach. We predicted that high-WMC individuals would rely more on proactive control processes, such that the last segment of the RT delta-plot would be less negative as compared as compared to the low-WMC individuals. We expected WMC-related differences to be most evident in the most cognitively demanding 25%-repetition condition, because WMC-related differences in performance are most likely to be apparent when the need for cognitive control is high (Engle, 2010).

Method

Participants. One hundred ninety-three University of Groningen first-year psychology students performed the Simon task. At least a week prior to performing the Simon task each participant completed an automated version of the Operation and Symmetry span tasks (Kane et al., 2004; Unsworth et al., 2005). Sample size was based on previous studies in which WMC measures were correlated with performance in conflict tasks (N = 148 in Keye et al., 2009; N = 99 and N = 112 in Morey et al., 2012; N = 122 and N = 108 in Weldon et al., 2013). Operation and Symmetry span scores were computed using the partial-credit scoring method recommended by Conway, Kane, Bunting, Hambrick, Wilhelm, and Engle (2005). This method counts the number of items recalled in the correct serial position regardless of whether the whole list was remembered correctly. For each participant, a composite WMC score was computed by averaging normalized Operations span (M = 58.58, SD = 13.04, range 16-75, where 75 is the maximum) and Symmetry span (M = 29.68, SD = 6.82, range 9-42, where 42 is the maximum) scores. Note that Operation and Symmetry span scores in our study are comparable to the normative data reported by Redick et al. (2012): N = 6236, M = 57.36, SD = 13.65 (Operation span) and N = 6018, M = 27.87, SD = 8.26 (Symmetry span). The data from one participant was excluded from the analyses due to a high rate of non-response trials (7.3%), one due to extremely slow responses (mean RT longer than 3 SD from the mean of all participants) and 10 due to high-error rates (15.63 – 24.65%), leaving 181 participants (123 females; 17-33 year old, M = 20.03, SD = 2.04) for analysis. All participants provided informed consent, received partial course credit or 7 euros for their participation, and had normal or corrected-to-normal vision.

Approximately half of the participants were assigned to the 75%-first order (in which the 75%-, 50%-, and 25%-repetition conditions were presented successively) and half to the 25%-first order (in which the 25%-, 50%-, and 75%-repetition conditions were presented successively). The mean WMC composite score was 0.05 (SD = 0.80, N = 90) for the 75%-first participants and -0.05 (SD = 0.91, N = 91) for the 25%-first participants, with no significant difference between the two (t(179) = 0.83, p = .408).

WMC Screening. In the automated version of the Operation span task (Unsworth et al., 2005), participants attempt to memorize 75 letters, presented in lists of 3 to 7 letters, while solving arithmetic problems. On each trial, participants first see an arithmetic equation (e.g., 2 + 7 = ?), the presentation time of which is adjusted for each participant during a practice session. Next, a one or two digit number is displayed until participants indicate whether the number is the answer to the arithmetic problem. Finally, a letter for later recall is displayed for 1 s. At recall, which occurs at the end of each list, participants are presented with a 4 x 3 matrix containing a subset of 12 letters of the alphabet, accompanied by an on-screen button marked "blank", and are to click on the letters in the order in which they were presented (pressing "blank" whenever a letter cannot be recalled). After each trial, a feedback screen with the number of correctly recalled items and mistakes on the arithmetic task is presented. The presentation order of the lists of different lengths, the equations to be solved, and the letters used in each list are randomized for each participant.

In the symmetry span task, participants are instructed to memorize 42 spatial locations of serially presented red squares in a 4 x 4 grid, while judging the vertical symmetry of a pattern made up of black squares presented in an 8x8 grid. On each trial, participants first see a black-square pattern, the presentation time of which is adjusted for each participant during a practice session. On a subsequent screen, they indicate whether the just-seen pattern was symmetrical. Finally, a red square for later recall is presented for 1 s. On each trial, 2-5 different locations and black-square patterns are presented. At recall, participants are presented with 4 x 4 grid on which they are to click to indicate the positions in which the red squares were presented in the order in which they occurred. After each trial, feedback on the number of correctly recalled positions and correctness of the symmetry judgement is presented. Participants who failed to reach 85% accuracy on the arithmetic and symmetry tasks were not invited to participate in the Simon task.

Simon task. Stimulus presentation and response registration were controlled by a program written in Matlab using the Psychtoolbox library (Brainard, 1997) and run on IBM compatible computers. The stimuli were presented on a 17-inch CRT monitor with a resolution of 1024 x 768 pixels at the unconstrained viewing distance of approximately 70 cm.

Stimuli for the Simon task were white squares and circles each measuring 2.2 x 2.2 cm across (subtending approximately 2° visual angle) presented on a black background 4.5 cm (approximately 5° of visual angle) to the left or right of a fixation cross. One stimulus was shown on each trial; each stimulus was presented an equal number of times to the left and right of fixation. Each trial began with the presentation of the fixation cross for 500 ms (such that the time between a response on one trial and the presentation of the stimulus for the following trial was 500 ms). The stimulus then was presented and remained in view until a response was made or a deadline of 1500 ms was exceeded. Half of the participants responded to the square by pressing the "x" key with the left index finger and to the circle by pressing the ">" key with the right index finger; the other half of the participants used the opposite mapping of stimuli to response keys.

The overall probability of congruent and incongruent trials, as well as the proportion of left- and right-hand responses was kept equal in each condition. The conditional probability of congruency repetitions (cC and iI trials) was manipulated to create three experimental conditions. In the 75%- repetition condition, cC and iI trials together comprised 75% of all trials in the block (i.e., in only 25% of trials did congruency on one trial not match the congruency of the previous trial), in the 50%- and 25%-repetition conditions the proportion of congruency repetitions was 50% and 25%, respectively.

Procedure. Participants were tested individually in dimly lit rooms. They were instructed to respond as quickly and as accurately as possible without making too many errors and were told to try to keep their accuracy above 90%. The task consisted of 70 practice trials and 1440 experimental trials. For the first 10 practice trials, feedback was given on each trial; the remaining 60 practice trials were divided into three blocks of 20 trials each with feedback (mean RT and accuracy) provided after each block. Each of the three experimental conditions consisted of eight blocks of 60 trials each, with feedback provided at the end of each block. The experimental conditions were presented in one of two possible orders: 75%-50%-25% (hereafter referred to as the 75%-first order) or 25%-50%-75% (25% first). Participants were assigned randomly to the two possible orders of the conditions with the constraint that each order was performed approximately equally often by both high- and low-WMC individuals. Participants were allowed to take breaks after each block and were required to take a 5-min break after each condition. The experiment lasted approximately 1 hour.

Data Analysis. The first trial of each block was considered a warm-up trial and removed prior to analysis. Trials on which no response was made within the time limit of 1500 ms, anticipatory responses (RTs faster than 100 ms) and responses that fell outside ffl 3 standard deviations of the mean were excluded from the RT data analysis (on average 1.79 % of trials). The RT data-trimming procedure was performed separately for each participant, experimental condition, and trial type (congruent vs. incongruent). Incorrect responses (on average 7.5 % of trials per subject) were excluded from the analysis of RT. Mean RTs for correct responses and percentage error were analysed with mixed ANOVAs. The Greenhouse-Geisser correction was applied where appropriate, but original degrees of freedom are reported for clarity.

In addition to analyses of mean accuracy and RT, distributions were analysed using delta-plots and conditional accuracy functions (CAFs). For this purpose, trimmed RTs of all trials (including both correct and incorrect responses) were rank-ordered and divided into five bins (quintiles) separately for each participant, each experimental condition (75%, 50% and 25% congruency repetition), each trial type (congruent and incongruent), and each presentation order (75% first and 25% first). Delta-plots were constructed by plotting the average Simon effect on the y axis as a function of response speed for each quintile on the x axis. Similarly, CAFs were created to visualize accuracy as a function of response speed by plotting accuracy on the y axis as a function of response speed for each quintile of the RT distribution on the x axis.

Results

Four WMC groups (low, middle-low, middle-high, and high) were formed using a quartile split of composite WMC score. Differences in the Simon effect and CSEs in 75%, 50%, and 25% congruency-repetition conditions as a function of WMC was evaluated by submitting mean RTs and percentage error to separate mixed ANOVAs with condition (75%-, 50%-, or 25%-repetition condition), congruency (congruent or incongruent) and previous trial congruency (congruent or incongruent) as within-subject factors, and WMC group and order of experimental conditions (25% first or 75% first) as between-subject factors.

Reaction time. There was a main effect of congruency (F (1, 173) = 555.18, MSE = 220,884, p < .001, η^2_p = .76) reflecting a typical Simon effect (i.e., slower RTs on incongruent (M = 410 ms) than on congruent trials (M = 390 ms)). The main effect of condition was also significant (F(2, 346) = 16.73, MSE = 7,799, p < .001, η^2_p = .09), with faster responses in the 50%-repetition condition than in the 75%- and 25%-repetition conditions (ps < .001), RTs between which did not significantly differ (ps = .72). The Condition x Congruency interaction was marginally significant (F(2, 346) = 3.06, MSE = 276.31, p = .051, η^2_p= .02), reflecting a trend for the size of the Simon effect to decrease as the proportion of congruency repetitions decreased (22 ms, 20 ms, and 19 ms for the 75%-, 50%-, and 25%-repetition conditions respectively). The main effect of previous trial congruency, although significant (F(1, 173) = 37.07, MSE = 3,263, p < .001, η^2_p = .18), was small (M = 399 ms vs. M = 401 ms for trials preceded by congruent vs. incongruent trials). More importantly, the Previous Trial Congruency x Congruency interaction (F(1, 173) = 2414.15, MSE = 960,844, p < .001, η^2_p = .93) was significant, reflecting typical CSEs, with a positive Simon effect of 62 ms following congruent trials and a reverse Simon effect of -22 ms after incongruent trials. The Previous Trial Congruency x Congruency x Condition interaction (F(2, 346) = 427.08, MSE = 45,322 , p < .001, η^2_p = .71) was significant, such that the size of the CSEs decreased linearly as the proportion of congruency repetitions decreased (polynomial linear trend, F(1, 173) = 597.02, MSE = 87,830, p < .001, η^2_p = .76). Because it is conceivable that the observed changes in the size of CSEs as a function of condition could be the result of the high proportion of exact stimulus-response repetitions in the 75%-repetition as compared to the 25%-repetition condition, the analysis was repeated excluding exact stimulus-response repetitions. Robust CSEs were still found as indicated by a significant Previous Trial Congruency x Congruency interaction (F(1,173) = 386.88, MSE =391,064, p < .001, η^2_p = .69), which was modulated by condition (F(2,346) = 274.55, MSE =45,284, p < .001, η^2_p = .61).

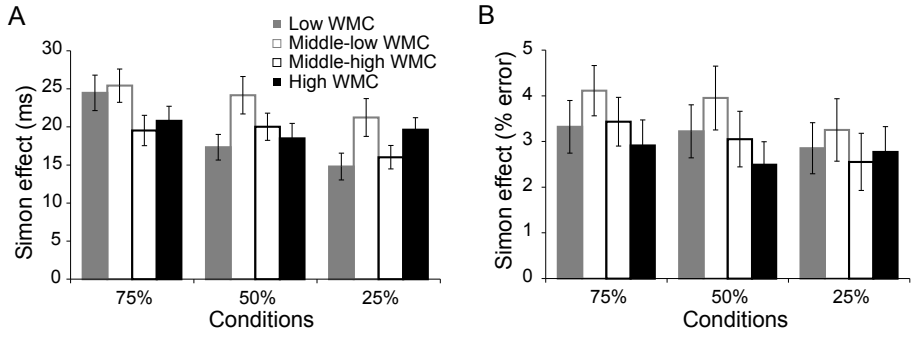

Figure 2.1. (*A*) Mean Simon effect for RT (incongruent RT – congruent RT) and (*B*) accuracy (incongruent percentage error – congruent percentage error) as a function of congruency repetition condition and WMC group. Error bars reflect the standard error of the mean.

The main effect of WMC was significant ($F(3, 173) = 2.67$, $MSE = 36{,}406$, $p = .049$, $\eta^2_p = .04$). Post-hoc Bonferroni-corrected comparisons revealed that the effect was driven by marginally significant RT differences between the low- and high-WMC groups ($p = .06$), with no significant differences between other WMC groups ($ps > .25$). There was a significant Condition x Congruency x WMC interaction ($F(6, 346) = 2.36$, $MSE = 213.11$, $p = .030$, $\eta^2_p = .04$). A follow-up analysis showed that whereas the Simon effect (Figure 2.1A) did not significantly differ between conditions for the middle-low-, middle-high-, and high-WMC groups (ps from .07 to .516), it did for the low-WMC group ($F(2, 88) = 14.42$, $MSE = 567.18$, $p < .001$, $\eta^2_p = .25$). Such group differences in the Simon effect as a function of condition could have been driven by differences in performance on congruent or incongruent trials. Thus, two separate three-way ANOVAs were conducted, with condition as a within-subject factor, and WMC and order as between-subject factors. For congruent trials, there was a significant WMC x Condition interaction ($F(6, 346) = 2.51$, $MSE = 396.64$, $p = .022$, $\eta^2_p = .04$), whereas for incongruent trials there was not ($F < 1$). The Previous Trial Congruency x Congruency x WMC interaction was not significant ($F(3, 173) = 1.69$, $MSE = 673.10$, $p = .171$, $\eta^2_p = .03$); and remained non-significant after exact stimulus-response repetitions were excluded ($F < 1$). For comparison with the results of Weldon et al. (2013), we computed two-tailed Pearson's correlation coefficients between the Simon effect on post-congruent and post-incongruent trials and the WMC measures (composite WMC, Operation, and Symmetry span scores). Significant positive correlations between the WMC measures and the Simon effect were found only for post-incongruent trials in the 25%-repetition condition ($r(179) = .237$, $p = .001$; $r(181) = .245$, $p = .001$; and $r(181) = .162$, $p = .03$, for composite WMC, Operation, and Symmetry span scores respectively).

Although the main effect of order was not significant ($F < 1$), order did interact with condition ($F(6, 346) = 290.16$, $MSE = 135{,}277$, $p < .001$, $\eta^2_p = .63$). Follow-up Bonferroni corrected comparisons revealed that in the 75%-first order condition RTs did not significantly vary over the course of the experiment ($ps = 1.0$; 393 ms, 394 ms, and 393 ms for the 75%-, 50%-, and 25%-repetition conditions respectively), whereas for the 25%-condition they decreased ($ps < .001$; 426 ms, 397 ms, and 375 ms for the 25%-, 50%-, and 75%-repetition conditions respectively). Moreover, RTs were slower in the first condition when the experiment started with the 25%-repetition condition as compared to when it started with the 75%-repetition condition ($t(179) = -6.25$, $p < .001$). There was also a significant Previous Trial Congruency x Congruency x Order interaction ($F(1, 173) = 10.65$, $MSE = 4{,}237$, $p = .001$, $\eta^2_p = .06$), indicating that CSEs were smaller in the 25%-first order as compared to the 75%-first order. The Previous Trial Congruency x Condition x Order interaction was significant ($F(2, 346) = 4.84$, $MSE = 344.87$, $p = .008$, $\eta^2_p = .03$), but showed no clearly discernible pattern. Finally, there was a significant Previous Trial Congruency x Congruency x Condition x Order interaction ($F(2, 346) = 33.85$, $MSE = 3{,}591$, $p < .001$, $\eta^2_p = .164$). No other interactions were significant (ps from .171 to .978).

Accuracy. The main effects of congruency ($F(1, 173) = 157.00$, $MSE = 0.64$, $p < 0.001$, $\eta^2_p = .48$) and condition ($F(2, 346) = 297.01$, $MSE = 0.72$, $p < .001$, $\eta^2_p = .63$) were significant, reflecting fewer errors on congruent ($M = 6.9\%$) than on incongruent trials ($M = 10.3\%$), and increasing accuracy as the proportion of congruency repetitions decreased (mean PE = 11.5%, 8.0%, and 6.3%, for the 75%-, 50%-, and 25%-repetition conditions, respectively). The Congruency x Condition interaction was significant ($F(2, 346) = 18.03$, $MSE = 0.019$, $p < .001$, $\eta^2_p = .09$), such that the Simon effect increased as the proportion of congruency repetitions increased (see Figure 2.1B). A small but significant effect of previous trial congruency ($F(1, 173) = 57.58$, $MSE = 0.089$, $p < .001$, $\eta^2_p = .25$) seems to reflect speed-accuracy trade-off, as trials preceded by congruent trials were slightly less accurate ($M = 9.2\%$) but faster than trials preceded by incongruent trials ($M = 8.0\%$). The Previous Trial Congruency x Condition interaction was significant ($F(2,326) = 19.37$, $MSE = 0.018$, $p < .001$, $\eta^2_p = .10$), reflecting that differences in accuracy between trials preceded by congruent as compared to incongruent trials decreased as the proportion of congruency repetitions decreased.

The significant Previous Trial Congruency x Congruency interaction ($F(1, 173) = 876.48$, $MSE = 5.55$, $p < .001$, $\eta^2_p = .84$) reflects the typical CSE: The Simon effect after congruent trials (13.5%) was positive and after incongruent trials was reversed (-6.7%). As in the RT analysis, the significant Previous Trial Congruency x Congruency x Condition interaction reflects a decrease in the size of the CSEs as the proportion of congruency repetition trials decreased ($F(2, 346) = 349.40$, $MSE = 0.84$, $p < .001$, $\eta^2_p = .67$; polynomial linear trend: $F(1,173) = 462.39$, $MSE = 1.18$, $p < .001$, $\eta^2_p = .73$). No evidence for differences in the CSEs were found between the high- and low-WMC groups ($F < 1$).

Although the main effects of WMC and order were not significant ($F < 1$), order interacted with condition ($F(2, 346) = 10.46$, $MSE = 0.02$, $p < .001$, $\eta^2_p = .06$), reflecting less accurate responses for both 75%- ($t(179) = -2.104$, $p = .037$) and 25%-congruency repetition conditions ($t(179) = 2.92$, $p = .004$) when encountered as the last condition in the experiment than when it was presented as the first.

Post-hoc power analyses. To evaluate whether the study had enough power to reveal WMC-related differences in conflict processing, a post-hoc power analysis using G*Power Version 3.1 was performed (Faul, Erdfelder, Lang, & Buchner, 2007). The analysis revealed that for the Congruency x Condition x WMC group x Order interaction with an alpha level of .05, $N = 181$, and correlation between repeated measures of .8 (based on the average correlation coefficient that was observed among the repeated measures) the statistical power to detect medium effects ($f = .25$) was 1.0, and that to detect small effects ($f = .10$) was .99. Additional analysis with the correlation between repeated measures set to .58 (the smallest observed correlation between repeated measures) revealed a power of 1.0 and .78 to detect medium and small effects, respectively. Note that previously reported WMC-related effects in conflict tasks were small to medium in size (e.g. Kane & Engle, 2003; Weldon et al., 2013). Thus, with 181 participants, of the effect sizes expected we had sufficient power (i.e., power of .8) to detect effects.

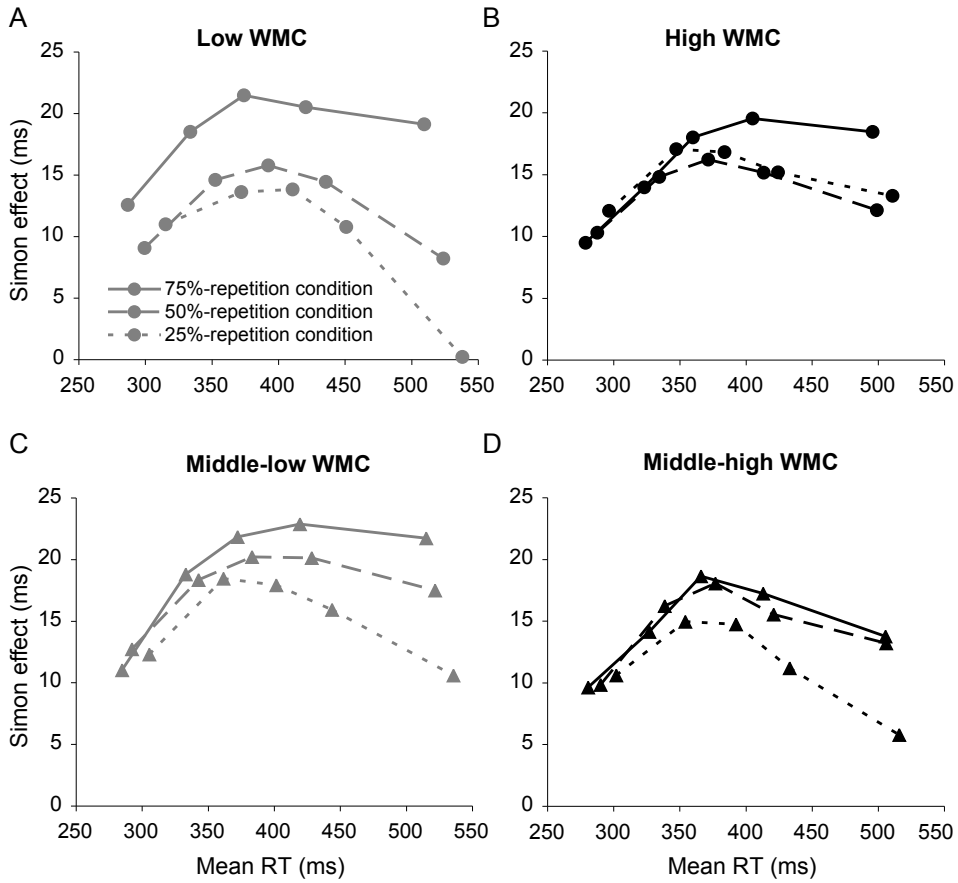

Figure 2.2. Delta-plots for RT as a function of congruency repetition condition for low (*A*), middle-low (*C*), middle-high (*D*), and high (*B*) WMC groups.

RT distribution analysis. Delta-plots were created following the procedure described in the Method section to analyze the Simon effect across the RT distribution for each condition, order, and WMC group, separately. There were no significant effects involving order for the RT distribution analyses, therefore we collapsed across order for clarity (Figure 2.2). Of particular theoretical interest was the slope of the lines connecting the two slowest quintiles of the distributions (Q4 and Q5), which was computed as the difference between the Simon effect of Q5 and Q4 divided by the difference in RT between Q5 and Q4. A mixed ANOVA was performed on the slope of the line connecting Q4 and Q5 with condition (25%-, 50%- or 75%-repetition condition) as a within-subject factor, and WMC group (4 bins) as a between-subjects factor.

There was a main effect of condition ($F(2, 354) = 3.57$, $MSE = 0.104$, $p = .029$, $\eta^2_p = .02$), with the slope of the last quintile being the most negative in the 25%-repetition condition ($M = -.068$), intermediate in the 50%-repetition condition ($M = -.044$), and the least negative in the 75%- repetition condition ($M = -.020$). The main effect of WMC ($F(1, 177) = 1.78$, $MSE = 1.05$, $p = .154$, $\eta^2_p = .03$) and the Condition x Group interaction were not significant ($F < 1$)[1]. As for the mean RT analysis, separate ANOVAs with condition as a within-subjects factor were performed for each WMC group. Consistent with visual impressions (see Figure 2.2A), there was a marginally significant main effect of condition for the low-WMC group ($F(2, 88) = 2.70$, $MSE = 0.10$, $p = .073$, $\eta^2_p = .06$), but the effect of condition was not significant for any other WMC group (ps .521, .364, and .771 for middle-low, middle-high, and high-WMC groups respectively).

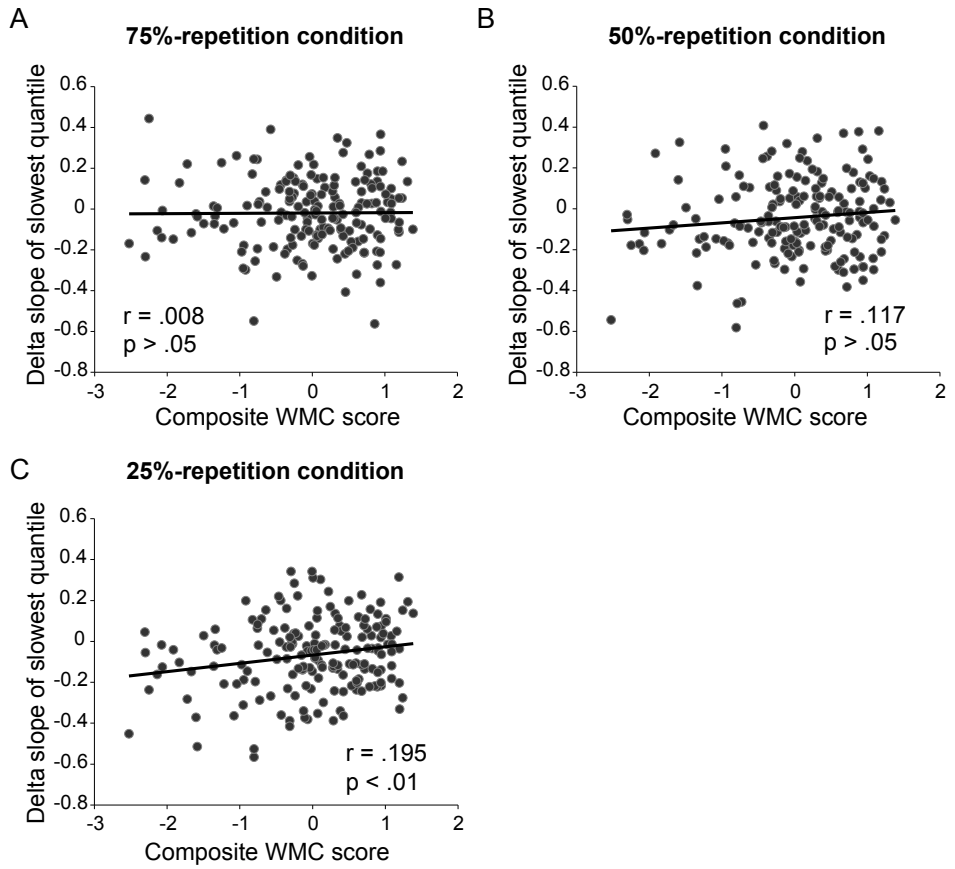

Figure 2.3. Pearson correlations derived from 181 participants between the slope of the last segment of RT delta-plots and composite WMC score for (*A*) 75%-, (*B*) 50%-, and (*C*) 25%-repetition condition. Each dot represents single subject data.

The relationship between WMC and conflict resolution was tested by computing two-tailed Pearson's correlation coefficients between WMC measures (composite WMC, Operation, and Symmetry span scores) and the slope of the last quintile in each experimental condition (Figure 2.3). The correlations are reported in Table 2.1. All WMC measures correlated with the slope of the last quintile in the 25%-repetition condition, but not in the 50%-, nor in the 75%-repetition condition.

[1] A delta-plot analysis conducted after error trial removal yielded comparable results to those reported with error trials included. The main effect of condition was significant ($F(2, 354) = 3.74$,

Table 2.1. Pearson's correlations between the slope of the slowest quantile in RT distributions and WMC measures (*N* = 181).

Measure	**1.**	**2.**	**3.**	**4.**	**5.**
1. Δ slope 75% condition					
2. Δ slope 50% condition	.168*				
3. Δ slope 25% condition	-.039	.121			
4. Composite WMC score	.008	.117	.195**		
5. Operation span score	.003	.111	.185*	.857**	
6. Symmetry span score	.011	.090	.149*	.857**	.470**

* p < 0.05; ** p < 0.01

Accuracy distribution analysis. Conditional accuracy functions were created following the procedure described in the Method section for each condition, order, and WMC group. From a theoretical standpoint, we were interested only in differences in accuracy at the fastest quintile. **Two separate mixed ANOVAs for congruent and incongruent trials were therefore performed on accuracy at the fastest quintile with condition (25%-, 50%- or 75%-repetition condition) as a within-subject factor and WMC group (high or low) as a between-subjects factor. As for the RT distribution analysis, we collapsed across order as there were no significant effects involving order (Figure 2.4).**

For congruent trials, there was a main effect of condition ($F(2, 354) = 6.41$, $MSE = 0.025$, $p = .002$, $\eta^2_p = .035$), with accuracy being the lowest in the 50%-repetition condition (86%), intermediate in the 75%-repetition condition (88%), and the highest in the 25%-repetition condition (89%). The main effect of WMC group and the Condition x WMC group interaction were not significant ($F < 1$). For incongruent trials, there was also a significant effect of condition ($F(2, 354) = 41.28$, $MSE = .035$, $p < .001$, $\eta^2_p = .189$), with accuracy being the lowest in the 75%-repetition condition (61%), intermediate in the 50%-repetition condition (63%), and the highest in the 25%-repetition condition (69%). The main effect of WMC group and the Condition x WMC group interaction were not significant ($F < 1$). As in the RT distribution analysis, WMC measures (composite WMC, Operation, and Symmetry span scores) were correlated with accuracy at the fastest quintile of CAFs. These correlations are reported in Table 2.2. No significant differences involving WMC and accuracy at the fastest quintile were observed for either congruent or incongruent trials.

MSE = .12, $p = .025$, $\eta^2_p = .02$). The main effect of WMC group ($F(1, 177) = 1.87$, MSE = .08, $p = .137$, $\eta^2_p = .03$) and Condition x WMC ($F < 1$) were not significant.

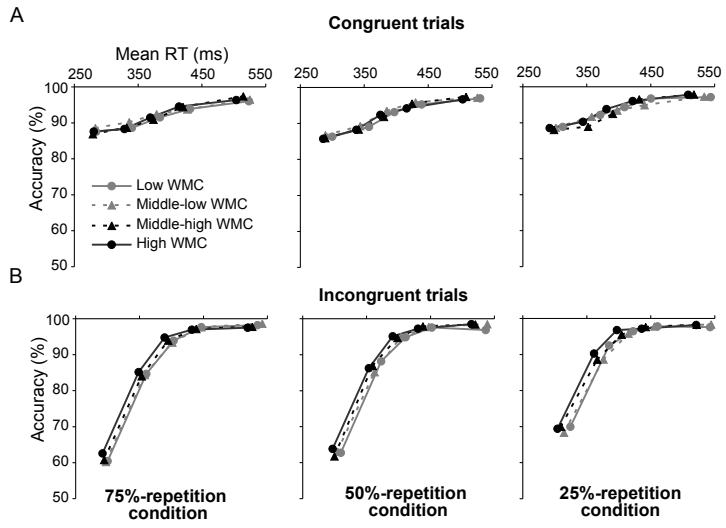

Figure 2.4. Conditional accuracy functions for congruent (*A*) and incongruent (*B*) trials as a function of WMC and congruency repetition condition.

Table 2.2. Pearson's correlations between the slope of the fastest quantile in RT distributions and WMC measures (*N* = 181).

Measure	**1.**	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**
1. Accuracy 75% condition (C trials)								
2. Accuracy 50% condition (C trials)	.526**							
3. Accuracy 25% condition (C trials)	.416**	.630**						
4. Accuracy 75% condition (I trials)	.414**	.412**	.404**					
5. Accuracy 50% condition (I trials)	.366**	.338**	.398**	.739**				
6. Accuracy 25% condition (I trials)	.209**	.318**	.413**	.656**	.733**			
7. Composite WMC score	-.042	-.034	-.016	.008	-.02	-.042		
8. Operation span score	-.031	-.038	-.016	-.001	-.075	-.095	.857**	
9. Symmetry span score	-.042	-.021	-.012	.013	.039	.022	.857**	.470**

* p < 0.05; ** p < 0.01

Discussion

The goal of the present study was to investigate how local variation in the need to exercise cognitive control to resolve conflict differentially affects individuals of high versus low WMC. In order to test whether the proficiency of conflict resolution is related to WMC (as suggested by Kane & Engle, 2003; Meier & Kane, 2012) we used the Simon task and kept the number of congruent and incongruent trials equal across conditions in order to minimize the need to actively maintain the task goal. The difficulty of trial-by-trial conflict resolution was manipulated across conditions by changing the proportion of congruency repetition trials. Participants were tested in each of three conditions: a 25%-repetition condition, in which demands for trial-to-trial adjustments in cognitive control are high, a 50%-repetition condition in which adjustments are less frequently called for, and a 75%-repetition condition which should impose relatively low demands on cognitive control processes. We reasoned that if the time-course of the conflict resolution depends on WMC, WMC-related differences should be especially evident in the 25%-repetition condition that imposes the highest demands on cognitive control. That the 25%-repetition condition indeed required higher levels of cognitive control as compared to other conditions was reflected by longer RTs when the experiment started with the 25%-repetition condition than when the 75%-repetition condition was presented first. Furthermore, RTs were stable across conditions in the 75%-first order and monotonically decreasing RTs in the 25%-first order, suggesting that practice effects in the 75%-first order were counteracted by an increase in condition difficulty over the course of the experiment.

The overall Simon effect was of similar magnitude for all participants. However, differences in how control was exercised were evident. Most notably, whereas for the high-WMC group (participants with scores in the fourth quartile of the composite WMC score distribution) the size of the Simon effect was relatively constant across conditions, for the low-WMC group (first quartile of the composite WMC score distribution) the Simon effect decreased as the proportion of congruency repetition trials decreased (i.e., as the need for trial-to-trial adjustments in cognitive control increased). Importantly, the reason why the Simon effect was smaller for low-WMC individuals in conditions with fewer congruency repetitions is that responses on congruent trials were relatively slow. Low-WMC individuals seemed to be especially ill-equipped to be able to take advantage of the presence of the irrelevant but correct stimulus location information on congruent trials when it was presented in the context of frequent congruency alternations. That is, it seems that low-WMC individuals were prone to inhibit essentially all automatic activation of responses from the irrelevant location dimension when there were many congruency alternations. Note that similar findings have been reported in an anti-saccade task (Unsworth et al., 2004). Unsworth et al. found that low-WMC participants were slower and more error-prone in the anti-saccade task than were high-WMC participants, but the two groups did not differ in a pro-saccade task in which responses could be made relatively automatically. When pro-saccade trials were mixed with anti-saccade trials, however, the low-WMC group performed more poorly than the high-WMC group on both types of trials. Kane and Engle (2003, Experiment 4) also presented evidence of WMC-dependent effects on congruent trials (although these effects were not statistically tested) in a Stroop task in which the proportion of congruent trials in a block was manipulated. The finding of a relation between WMC and factors such as the proportion of congruent trials and congruency repetitions on the responses made on congruent trials suggests that WMC-related differences in interference-task performance extend beyond the resolution of response conflict.

The analysis of sequential effects revealed a large positive Simon effect after congruent trials and a reverse Simon effect following incongruent trials, but no interaction between WMC group and the size of the CSEs. Weldon et al. (2013) reported that low- as compared to high-WMC individuals showed bigger CSEs, and the effect was driven both by a bigger positive Simon effect after congruent (cI-cC) and a bigger reverse Simon effect after incongruent trials (iI-iC). Our post-hoc analyses conducted to allow comparison to Weldon et al.'s study showed that although low WMC was associated with a bigger reverse Simon effect after incongruent trials (iI-iC trials) in the 25%-repetition condition, no other effects were significant. Our failure to fully replicate the effects reported by Weldon et al. (2013) can most likely be attributed to differences in the response-stimulus interval (RSI) used (1000 ms vs. 500 ms in our study). As previously shown (Egner, Ely, & Grinband, 2010), the size of CSEs varies considerably as a function of RSI.

The RT distribution analysis revealed a gradual increase in the Simon effect followed by a gradual decrease in the effect across the RT distribution (cf. Burle, Possamai, Vidal, Bonnet, & Hasbroucq, 2002; Ridderinkhof, 2002a; Wylie et al., 2010). More importantly with respect to the question of documenting differences in cognitive control, correlation analyses between the slope of the last segment of the RT delta-plots and the WMC measures revealed that low WMC scores were associated with a steeper negative-going delta-plot slope in the 25%-repetition condition. Taking into account that the steepness of the slope reflects the strength of reactive control, this finding suggests that low-WMC individuals tend to exercise reactive conflict resolution even in the most demanding 25%-repetition condition. The finding that WMC measures and the slope of the last segment of the delta-plots did not correlate in the 75%- and 50%-repetition conditions are consistent with the dual mechanisms of control framework that distinguishes reactive and proactive modes of cognitive control (for a review, see Braver, 2012). According to this framework, control is reactive when task goals are reactivated by the environment after conflict is encountered, whereas in the proactive control mode, task goals are actively maintained to suppress irrelevant information. Because proactive control is resource-demanding, it is assumed to be most likely employed by individuals having sufficient cognitive resources, and limited to task contexts in which interference is frequent and can reliably be expected. Thus, in the context of "dual mechanisms of control", no differences in delta-plot patterns between high- and low-WMC individuals would be expected in the 75%- and 50%-repetition conditions, because reactive control should be sufficient to support adequate task performance.

The pattern of a general increase in the Simon effect followed by a decrease across the RT distribution has been interpreted in terms of automatic activation of the spatially corresponding response triggered by the task-irrelevant stimulus dimension, the strength of which decreases over time (De Jong et al., 1994). Whether the decrease in the strength of the activation of the spatially corresponding response is a result of passive decay or active inhibition is a matter of debate (for a review, see Proctor et al., 2011). According to the activation-suppression hypothesis (Ridderinkhof, 2002), the decrease in the Simon effect as a function of response time reflects active suppression of the incorrect response. Such suppression of the spatially corresponding response allows the making of relatively fast responses on incongruent trials, but slows down responding on congruent trials for which response suppression is not needed, thus resulting in a small or even reverse Simon effect when responses are relatively slow. The slope of the slowest portion of the delta-plot thus,

according to this reasoning, reflects the strength of suppression of spatially corresponding responses, or reactive control (Forstmann, Jahfari et al., 2008; Forstmann, van den Wildenberg et al., 2008; Ridderinkhof, 2002; Winkel et al., 2011; Wylie et al., 2010).

Reaction-time distribution analyses, as well as changes in the Simon effect across conditions in the low- but not the high-WMC group suggest that low-WMC individuals indeed relied more on reactive recruitment of cognitive control and thus were more sensitive to the task context than were high-WMC individuals who exercised control proactively. It has also been proposed that a smaller percentage of errors in the fastest portion of the distribution can be considered an index of proactive control (Wylie et al., 2010). However, neither others nor we have found significant relation between WMC and error rates at the fastest portion of the RT distribution (e.g. Heitz & Engle, 2007; Kane & Engle, 2003). In Heitz and Engle's study, although the effects were not statistically tested, a graphical representation of the results shows no group differences. Similarly, Fukuda and Vogel (2011) reported that high- and low-WMC individuals were equally susceptible to attentional capture by distracting information, although high-WMC individuals were faster to recover from it.

Although the finding of a more negative-going slope for low-WMC individuals is consistent with greater inhibition and reliance on reactive control in conflict resolution (Ridderinkhof, 2002a, 2002b), some researchers have interpreted WMC-related differences in the last segment of delta-plots in the Stroop and Eriksen flanker tasks as evidence for differences in goal maintenance abilities (Kane & Engle, 2003; Unsworth et al., 2011). Prior research suggests that temporary loss of the task goal is most likely when the task goal is not reinforced contextually (e.g., Kane & Engle, 2003; Long & Prat, 2002). In the present study, instances of intermittent loss of the task goal (e.g., "ignore stimulus location") could have possibly occurred in the 75%-repetition condition in which a maximum of 8 congruent trials (taking roughly 7 s to complete) could occur in a row. However, we did not find a significant correlation between the slope of the last delta-plot segment and WMC in the 75%-repetition condition (see Figure 2.3A, and Table 2.1). This suggests that the WMC-related differences observed in the current study were not primarily related to group differences in goal-maintenance abilities but rather reflect differences in conflict processing.

In conclusion, this study showed that WMC-related differences in interference effects are related not only to variability in goal-maintenance abilities, but also reflect variations in conflict processing, as previously proposed by Kane and Engle (2003). In a Simon task in which congruent and incongruent trials were equiprobable and the need to maintain task goals was minimal, RT distribution analysis revealed WMC-related differences in the dynamics of cognitive control. Moreover, changes in the conditional probability of congruency repetition trials affected the performance of low-WMC individuals, whereas high-WMC individuals were relatively insensitive to the task context. This finding shows that high-WMC individuals rely more on a proactive cognitive control strategy in tasks with high cognitive control demands, whereas low-WMC individuals are prone to resolve conflict reactively.

3 Neural mechanisms underlying superior attention control abilities

Individuals scoring relatively high on measures of working memory tend to be more proficient at controlling attention to minimize the effect of distracting information. It is currently unknown whether such superior attention control abilities are mediated by stronger suppression of irrelevant information, enhancement of relevant information, or both. Here we used steady-state visual evoked potentials (SSVEPs) with the Eriksen flanker task to track simultaneously the attention to relevant and irrelevant information by tagging target and distractors with different frequencies. This design allowed us to dissociate attentional biasing of perceptual processing (via SSVEPs) and stimulus processing in the frontal cognitive control network (via time-frequency analyses of EEG data). We show that while preparing for the upcoming stimulus, high- and low-WMC individuals use different strategies: High-WMC individuals show attentional suppression of the irrelevant stimuli whereas low-WMC individuals demonstrate attentional enhancement of the relevant stimuli. Moreover, behavioral performance was predicted by trial-to-trial fluctuations in strength of distractor-suppression for high-WMC participants. We found no evidence for WMC-related differences in cognitive control network functioning, as measured by midfrontal theta-band power. Taken together, these findings suggest that early suppression of irrelevant information is a key underlying neural mechanism by which superior attention control abilities are implemented.

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Dissociable mechanisms underlying individual differences in visual working memory capacity

NeuroImage, *in press*

Introduction

Control of attention is critical for keeping behaviorally relevant goals active (e.g., replying to an important email) and inhibiting distractions (e.g., checking Facebook). The ability to control attention to minimize distraction has been suggested to be the primary factor determining an individual's working memory capacity (WMC; Kane et al., 2007), a characteristic that predicts a range of cognitive abilities, from stimulus processing (Brumback et al., 2004; Tsuchida, Katayama, & Murohashi, 2012) to fluid intelligence (Cowan et al., 2005; Engle, Tuholski et al., 1999). Behaviorally, high- compared to low-WMC individuals are less susceptible to visual (Hutchison, 2011; Kane & Engle, 2003; Unsworth et al., 2004) and auditory (Conway et al., 2001) distractions in tasks that require attentional control. For example, low-WMC individuals, more often than high-WMC individuals, notice task-irrelevant salient stimuli such as their own name (Conway et al., 2001), and are slower to inhibit automatic reactions towards unexpected visual stimuli (Unsworth et al., 2004). However, the strength of the relationship between WMC and attentional control seems to be task- and context-dependent (Heitz & Engle, 2007; Keye et al., 2013; Keye et al., 2009; Sorqvist, Marsh, & Nostl, 2013; Wilhelm et al., 2013).

This frequently observed relationship between WMC and performance in attentional control tasks suggests that high- compared to low-WMC individuals are better able to suppress various sources of distraction. However, selective attention depends on two inter-related mechanisms: Suppression of irrelevant information and enhancement of relevant information (Andersen & Muller, 2010; Corbetta & Shulman, 2002; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Polk, Drake, Jonides, Smith, & Smith, 2008). It is unknown whether WMC-related differences in attention control reflect differences in suppression of irrelevant information (Hasher et al., 2007), or enhancement of relevant information (Heitz & Engle, 2007), or a combination of both.

Indirect evidence for WMC-related differences in suppression of irrelevant information is provided by cognitive aging studies (Gazzaley et al., 2008; Gazzaley, Cooney, Rissman, & D'Esposito, 2005). For example, Gazzaley and colleagues (2008) demonstrated age-related impairments in suppressing irrelevant information with no or weak changes in processing of relevant information. Moreover, they found that the decreased ability to suppress irrelevant information was related to impaired WM task performance, suggesting that the limited-capacity WM system was burdened with to-be-ignored irrelevant information. Although these findings may suggest that variations in WMC reflect differences in suppression of irrelevant information, cognitive aging effects are not limited to the WM system, thus leaving the question about the neural mechanisms related to WMC open.

Fukuda and Vogel (2009) studied the relationship between WMC and attentional control more directly by correlating WMC scores (as measured by change-detection task) with electrophysiological indices of attentional control. They reported WMC-related differences in early event-related potentials (ERPs) elicited by task-irrelevant probes at to-be-ignored locations, and interpreted such differences as a deficiency of low-WMC individuals to suppress distracting information. However, attention-related changes in early ERPs seem to reflect both suppression of irrelevant information and enhancement of relevant information (Couperus & Mangun, 2012), making it difficult to judge the relative contribution of these two processes in the Fukuda and Vogel (Fukuda & Vogel, 2009) results. Moreover, the WMC scores and electrophysiological indices of effectiveness of attentional control were derived

from the tasks that share many features (e.g., multiple-stimulus arrays and short stimulus presentation times), thus raising concerns about the generalizability of the reported effects to other experimental contexts (cf. Mall, Morey, Wolff, & Lehnert, 2014), and calling for the need to investigate how attentional control is related to WMC using other typical WMC measures such as complex span tasks (Kane et al., 2004; Unsworth et al., 2005).

We addressed these limitations by recruiting high- and low-WMC individuals – defined in a separate session based on performance on two complex-span tasks – to perform a modified version of an Eriksen flanker task. By simultaneously presenting targets and flankers at different flicker frequencies to elicit frequency-specific steady-state evoked potentials (SSVEPs) we were able simultaneously to track attention allocation to the relevant and irrelevant information on a single trial level (Scherbaum, Fischer, Dshemuchadse, & Goschke, 2011). SSVEP amplitude is enhanced when an object or a specific feature is attended, and suppressed when it is unattended, compared to passive viewing of flickering stimuli (Andersen & Muller, 2010). We were thus able to determine whether better attentional control exhibited by high-WMC individuals is mediated by a stronger enhancement of relevant sensory information, suppression of irrelevant sensory information, or a combination of both.

An alternative explanation for WMC-related differences in sensitivity to the distracting information is that high- and low-WMC individuals might process stimuli differently in a later stage, during response-selection. Note that the two accounts – reduced sensory processing of distracting information in early stages and differences in response selection stage – are not mutually exclusive, and both might contribute to any observed differences in behavioral performance. Response selection and related action monitoring processes have been studied with EEG by focusing on oscillatory activity in theta-band (4-8 Hz; Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013; Hanslmayr et al., 2008). Incongruent trials (e.g., EEFEE in the Eriksen flanker task), during which co-activation of competing action alternatives creates response conflict, are associated with increased theta-band activity in the frontal cognitive control network, which includes medial frontal and dorsolateral prefrontal areas (Cavanagh, Cohen, & Allen, 2009; Nigbur, Cohen, Ridderinkhof, & Sturmer, 2012). Given that WM processes are related to theta-band activity in frontal networks (Hsieh & Ranganath, 2014), and that WM and conflict tasks engage overlapping fronto-parietal networks (Nee et al., 2007; Niendam et al., 2012), we hypothesized that high- and low-WMC individuals might differ in conflict-related theta. More specifically, we predicted that high-compared to low-WMC individuals would show smaller differences between incongruent and congruent trials (interference effect) in theta-band power.

Method

WMC screening. Six hundred and eighteen University of Groningen first-year psychology students performed Operation span and Symmetry span tasks in a separate experimental session at least 5 months prior to the Eriksen flanker task. Previous studies showed high test-retest reliability of complex span tasks, with correlations between sessions ranging from .70 to .83 (Klein & Fiss, 1999; Unsworth et al., 2005).

In the Operation span task (Unsworth et al., 2005), participants attempted to memorize 75 consonants that are serially presented in 3-7 item lists. Presentation of each letter is followed by an arithmetic problem. In the symmetry span task (Kane et al., 2004), participants attempt to memorize 42 spatial locations of serially presented red squares in a 4 × 4 grid, while judging the vertical symmetry of a pattern made up of black squares presented in an 8 × 8 grid. On each trial, locations and patterns were presented in 2-5 item lists.

The scoring procedure was done using a partial-scoring method (Conway et al., 2005), according to which correctly recalled items are given a partial credit if they are listed in the correct serial position even if all the items in the list are not recalled correctly. All list lengths (3 to 7 items in the operation span task and 2 to 5 items in the symmetry span task) were weighted equally and proportion of correct responses was computed for each list length separately (e.g., 2 of 5 = 0.4, 3 out of 3 = 1.0). Thus obtained proportions were averaged across all lists. Individual WMC scores in operation span and symmetry span tasks thus could range from 0 to 1. For each participant, a composite WMC score was computed by averaging normalized operation span and symmetry span scores.

Participants. As the goal was to characterize a specific dimension of individual differences rather than to estimate the exact effect size, an extreme-groups design was used (Yarkoni & Braver, 2010). Only participants whose composite WMC score fell in the upper (high-WMC group) and the lower (low-WMC group) quartiles of the distribution of composite WMC scores (N = 618, $Q1$ = -0.41, $Q3$ = 0.60 of z-WMC) were invited to the EEG session to perform the Eriksen flanker task.

To determine the required sample size to obtain adequate power, we used a previous report on WMC-related differences in early attention sensitive visual evoked potential (P150) while participants performed the Eriksen flanker task (Brumback et al., 2004). To achieve 80% power with a significance level of α = 0.05, and an effect size of Cohen's d = 1.13 (calculated from the previous report; Brumback et al., 2004), the required number of participants per WMC group was 14 (t-test for differences between two independent means; Faul et al., 2007). However, as detectability of SSVEP amplitudes is also subject to individual differences (Fuchs, Andersen, Gruber, & Muller, 2008), we collected more data than indicated by the power analysis.

Participants were 23 high-WMC individuals (z-WMC = 0.98, SD = 0.18) and 24 low-WMC individuals (z-WMC = -1.38, SD = 0.53). Data from 14 participants were excluded: One due to poor behavioral performance and 4 because their SSVEP responses were not higher than the general noise level. Exclusion of other 9 participants was based on extensive eye-blink artifacts in more than 33% of all trials (range: 33-41%) that occurred during the critical pre-stimulus mask-to-response period. The fact that the pre-stimulus mask was presented for 1000 ms and an eye-blink can last for several hundred miliseconds meant that effective SSVEP entrainment was compromised on many trials. Note that in many other SSVEP studies, much longer stimulus presentation times are used (up to several seconds), making eye-blink artifacts less of a concern. Thus, 17 high-WMC (9 females, mean age 20.94, 4 left handed) and 16 low-WMC (14 females, mean age 21.31, 1 left handed) were included in the analysis. All participants had normal or corrected-to- normal vision. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee. Informed consent was obtained from all participants.

Task. An Eriksen flanker task with a four-to-two mapping of stimuli to responses was used (Wendt, Heldmann, Munte, & Kluwe, 2007). Stimulus presentation and response registration were controlled by a program written in Matlab using the Psychtoolbox library (Brain-

ard, 1997). Stimuli were displayed on a 17-inch CRT monitor (1024 x 768 pixels; 100 Hz refresh rate). White stimuli comprised of a target letter and four identical flanker letters (two on each side of the target) were presented against a black background. The stimuli were presented in Sloan font, letters of which are equally discriminable and for which height equals width (Pelli, Robson, & Wilkins, 1988). Viewing distance was 120 cm; each letter subtended 2.4° of visual angle, separated by 1.2° visual angle. Four letters (M, N, E, F) were mapped to two response keys. Speeded responses were to be made to the central target letter. Participants responded to the target letters M and E by pressing the "x" key with the left index finger and to N and F by pressing the ">" key with the right index finger. Only response congruent (e.g., M M M M M) and response incongruent (e.g., M M N M M) stimuli were used for the task. The overall probability of congruent and incongruent trials, as well as the proportion of left- and right-hand responses was kept equal. The task consisted of 50 practice and 640 experimental trials divided into 10 blocks with feedback (mean RT and accuracy) provided after each block. Participants were instructed to respond quickly while keeping accuracy levels around 90%. This was done to avoid ceiling effects in performance and to minimize the effect of individual differences in speed-accuracy tradeoff settings.

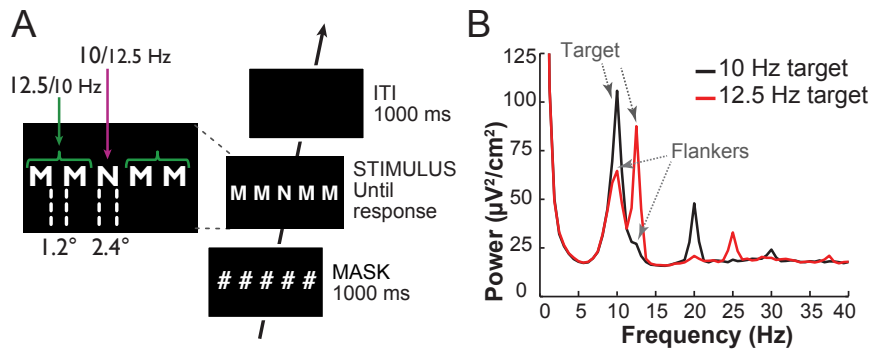

Figure 3.1. (A) Stimuli, task, and trial design. Modified version of the Eriksen flanker task showing an incongruent trial. Pre-stimulus mask (#####) and stimulus (MMNMM) were tagged with the same frequencies. (B) Frequency spectrum of the EEG signal averaged across all participants for the two frequency-tagging conditions: (1) 10 Hz target and 12.5 Hz flankers (black line), (2) 12.5 Hz target and 10 Hz flankers (red line). The subject-specific best-electrode was used in the plot.

Each trial started with a 1 s presentation of a pre-stimulus mask (# # # # #) with the central hash mark tagged with one frequency (e.g., 10 Hz) and the flankers with another (e.g., 12.5 Hz; see Figure 3.1). Hash marks were then replaced by the stimulus (with tagging frequencies identical to the pre-stimulus mask period), which remained on-screen until the response was made or a deadline of 2 s was exceeded. The SSVEPs were elicited by modulating the brightness of the stimuli by a square wave (50% of the cycle on, 50% of the cycle off). Tagging frequencies of the target and flankers were reversed after each block.

Behavioral data analyses. The first trial of each block, error trials (incorrect or no-response trials), trials with RTs faster than 150 ms, and responses that fell outside 3 standard deviations of the mean were excluded from the RT data analysis. The RT thresholding procedure

was performed separately for each participant, experimental condition (10 Hz and 12.5 Hz target), and trial type (congruent vs. incongruent). The differences between high- and low-WMC groups in behavioral performance were tested using repeated measures ANOVA with factors: Trial congruency (congruent and incongruent) and WMC group (high and low).

To quantify the evidence in favor of the "null effect" (non-significant results involving WMC group factor) by grading the decisiveness of the evidence (Jeffreys, 1961) we performed Bayesian analysis of variance (Rouder, Morey, Speckman, & Province, 2012). Non-significant results involving the WMC group factor were evaluated by comparing Bayes factors of two models (with and without the WMC group factor) that were computed using *lmBF* function from package *BayesFactor* package in R (Morey & Rouder, 2013; Rouder et al., 2012). Comparison of Bayes factors of models allows assessment of the amount of evidence present in the data in favor of any hypothesis, including the null hypothesis, which is not possible with conventional statistical analyses (Gallistel, 2009).

EEG recording and preprocessing. Sixty-two scalp EEG electrodes (Electro-cap International Inc., Eaton, Ohio, USA) were positioned according to the modified version of the international 10-20 system (6 additional electrodes were placed 10% below standard FT7, PO7, O1, FT8, PO8, and O2 electrode positions; F1, F2, CP1, CP2, FT7, and FT8 were not measured). Two additional reference electrodes were placed on the mastoids. Vertical and horizontal eye movements were recorded using four additional electrodes, two of which were placed below and above the left eye and the other two on the outer eye canthi. The data were recorded using an average reference REFA 8–72 amplifier (Twente Medical Systems, Enschede, The Netherlands). The data were digitally low-pass filtered at 140 Hz and sampled at 500 Hz. All offline data preprocessing and analysis was done using EEGLAB toolbox for Matlab (sccn.ucsd.edu/eeglab/) and custom written Matlab scripts.

The data were re-referenced offline to the average activity recorded at the mastoids and high-pass filtered at 0.5 Hz. Continuous EEG recording was epoched (-1 s to 3 s after pre-stimulus mask onset). The data were baseline corrected to the time window from -200 ms to the mask onset. Trials containing muscle artifacts or eye blinks during the time window of interest (the pre-stimulus mask onset to the response-execution) were manually removed. As it is common in SSVEP studies, the biggest proportion of rejected trials was due to eye blinks. The second step comprised of an independent component analysis, and components that did not account for any brain activity, such as eye movements (outside the time window of interest) or noise, were subtracted from the data. Extreme RT trials were also removed as described previously (see *Behavioral data analyses* section). The average number of trials per subject included in the analysis was 501.15 (*SD* = 49.84).

SSVEP analyses

Electrode selection. To select the appropriate electrode for SSVEP analysis, a subject-specific "best-electrode" approach was employed (Fuchs et al., 2008; Muller et al., 2003). For this purpose, artifact-free data were Laplacian transformed to increase topographical selectivity by filtering-out low spatial frequencies, which are considered to be a result of volume-conduction effects. Note that Laplacian transformation involves computation of the second spatial derivative, thus the units of EEG amplitude after transformation are $\mu V/cm^2$. Power (amplitude squared, $\mu V^2/cm^2$) at 10 and 12.5 Hz was estimated by FFT of the data in the time window from pre-stim-

ulus mask onset to 600 ms post-stimulus (separately for the 10 Hz target and 12.5 Hz target conditions). These power estimates were used to calculate the attention effect (the power of 10 Hz flankers was subtracted from the power of 10 Hz targets, the same was done for the stimuli tagged with 12.5 Hz). The two thus obtained values were averaged for each channel and used to create iso-contour voltage maps. For each participant, the occipital electrode that showed the largest overall attention effect was selected for the analysis (Figure 3.3C).

Computation of SSVEP amplitude. For the time-course analysis of SSVEP amplitudes, epoched data were concatenated (separately for 10 Hz and 12.5 Hz target conditions) to improve frequency resolution. Each time series was then filtered using narrow band-pass Gaussian filters with means of 10 and 12.5 Hz frequency and a standard deviation of 0.5 Hz. The filters were implemented by multiplying the FFT of the data by the exponential function:

$$e^{-0.5(f-f_0)^2/s^2},$$

where f is frequency, f_0 is the frequency of interest (10 and 12.5 Hz), and s is the specified standard deviation of the Gaussian, and then performing an inverse FFT. After filtering the data, the instantaneous amplitude at 10 and 12.5 Hz frequency was extracted using Hilbert transform. Subsequently, the epoched structure was recreated and averaged over trials. Trial average amplitude was baseline normalized to pre-mask period (-500 to -200 ms) by computing percent change of the amplitude at each time point relative to the average baseline interval amplitude. This normalization procedure was performed for two reasons: To remove scale differences between frequencies (power-law scaling) to allow comparison of 10 and 12.5 tagging frequency condition, and to eliminate scale differences between individuals allowing direct comparison between groups (Cohen, 2014; Roach & Mathalon, 2008). The relatively early baseline time window minimizes temporal leakage resulting from narrow filtering. Finally, baseline-corrected time series were averaged across 10 and 12.5 Hz conditions separately for targets and flankers.

Statistical analyses of SSVEP amplitudes. Two sets of statistical analyses were performed using a non-parametric cluster-based randomization procedure (Maris & Oostenveld, 2007). First, we assessed differences in target and flanker SSVEP amplitudes between WMC groups. Second, we compared changes in target and flankers SSVEP amplitude relative to the baseline separately for each WMC group.

In order to test our specific hypotheses concerning group differences in processing targets and flankers, the following steps were carried out for SSVEP amplitudes. First, independent samples t-tests were run comparing the SSVEP amplitude for high- and low-WMC groups at each time point from 0 to 1600 ms (where 0 is pre-stimulus mask onset). Second, a null hypothesis distribution was created at each time point by randomly assigning each participant to one of the two WMC groups, and t statistics were recomputed. This was repeated 500 times. Third, group differences in SSVEPs were considered statically significant if the actual t-value at that time point was greater than 95% of null t-values ($p < .05$, two-tailed). Fourth, cluster-based correction was applied to correct for multiple comparisons over time points. Clusters of contiguous time points were considered significant if the size of the cluster was bigger than expected under the null hypothesis at a significance level of $p < .05$. The null hypothesis distribution of cluster sizes was obtained by first thresholding the t-values obtained from each iteration of permutation testing at $p < .05$, and subsequently storing

the maximum cluster size observed at that iteration step. Finally, to obtain more stable estimates from permutation testing we ran a "meta-permutation test" by repeating the permutation procedure 20 times. The averaged results from 20 permutations, each consisting of 500 iterations, are reported here.

Target and flankers SSVEP amplitude comparison against the baseline was performed following a similar procedure. First, four one-sample t-tests (separate for each condition and group) were run comparing the SSVEP amplitude for each time point in the time-window from 0 to 1600 ms (where 0 is pre-stimulus mask onset) against zero. Second, a null hypothesis distribution was created for each time point. This was done by taking the data from a random number of participants, multiplying by -1 (this converts baseline-minus-data to data-minus-baseline), and recomputing the t-values. The procedure was repeated 500 times, separately for each condition and each group. Third, changes in SSVEP amplitude relative to the baseline were considered statically significant if the actual t-value at that time point was greater than 95% of null t-values (i.e., $p < .05/4$, corrected for multiple comparisons across conditions and groups). Finally, cluster-based correction was applied to correct for multiple comparisons over time points, and permutation tests were repeated 20 times (each consisted of 500 iterations).

Control analyses. The tagging frequencies (10 and 12.5 Hz) within the alpha band (8-13 Hz) were used to acquire easily detectable SSVEPs, as high flicker frequencies produce small SSVEPs that are difficult to distinguish from the general noise level (Herrmann, 2001). However, suppression in the upper alpha-band (10-13 Hz) power over occipital, parietal, and frontal areas has been associated with active stimulus processing (Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998), and has been shown to differ between high and low IQ individuals (Doppelmayr, Klimesch, Hodlmoser, Sauseng, & Gruber, 2005; but see Toffanin, Johnson, de Jong, & Martens, 2007). We therefore conducted additional analyses to test whether groups differed in endogenous task-related upper alpha suppression, to rule out an alternative interpretation of group differences in SSVEP amplitudes.

For upper alpha (10-13 Hz) power (amplitude squared) analysis the steps were identical to SSVEP amplitude computation, however a broader Gaussian filter with a mean of 11.5 and a standard deviation of 1 Hz was used to capture activity in the upper-alpha frequency range. The changes in alpha power are reported as percent change of the power at each time point relative to the pre-mask period (-300 to -100 ms). Statistical group comparisons in alpha-band power were performed using non-parametric cluster-based randomization procedure, as described previously (see *Statistical analyses of SSVEP amplitudes*).

Theta-band (3-7 Hz) power analyses. To extract theta-band activity, time-frequency decomposition was performed by convolving single-trial data from all electrodes with complex Morlet wavelets, defined as:

$$e^{i2\pi f_i t} e^{-t^2/(2\sigma^2)},$$

where t is time, f_i is frequency which ranged from 2 to 40 Hz in 40 logarithmically spaced steps, and σ is the width of each frequency band, which varied as a function of frequency $(4/(2\pi f_i))$ to obtain equally good frequency resolution at low and high frequencies. Instantaneous power was computed as the square of the complex convolution signal Z (*pow-*

er = real[z(t)]² + imag[z(t)]²) and averaged across trials. Further, power values were normalized by converting to the decibel scale using the formula:

$$10\log_{10}(power/baseline),$$

where -300 to -100 ms pre-mask period served as a baseline.

Statistical analysis of theta-band power. The FCz electrode for theta-band power analyses was selected based on previous reports (Cavanagh et al., 2009; Cohen & Cavanagh, 2011a; Nigbur et al., 2012) and was confirmed by qualitative analyses (Figure 3.5A, the inset topographical maps). Because conflict-related brain activity is linked both to stimulus processing and to response preparation (Cavanagh, Zambrano-Vazquez, & Allen, 2012), we separately tested changes in theta-band power time-locked to stimulus and response.

For stimulus-locked analysis, theta power values were averaged in a 300-650 ms time-window (where 0 is stimulus onset; Figure 3.5A), and for response-locked analyses in a -200-100 ms time-window (where 0 is response; Figure 3.5C). Thus obtained power values were submitted to two separate repeated measures ANOVA with factors: Trial congruency (congruent and incongruent) and WMC group (high and low). Non-significant results involving WMC group factor were subsequently evaluated by comparing Bayes factors from ANOVA models, as previously described (see *Behavioral data analyses* section).

Single-trial analyses. To evaluate the effect of WMC-related differences in attention deployment to the target and flankers on the behavioral performance, we used linear mixed effects (LME) models with log RT as a dependent variable (Pinheiro & Bates, 2000). Logarithmic transformation of RTs was done to correct for positive skew of the RT distributions (Heathcote, Popiel, & Mewhort, 1991). LME models are extensions of standard regression models and allow modeling of single-trial data using both fixed effects (e.g., experimental manipulations) and random effects (e.g., inter subject variability) and thus account for both within- and across-subject variance. The modeling was implemented using *lmer* function from package *lme4* in R version 3.03 (Bates et al., 2014). The *p*-values were estimated for each factor of the fitted model using *lmeTest* package (Kuznetsova, Brockhoff, & Christensen, 2013).

The best-fitting model was selected as follows. First, the base model was fitted, which included the fixed factors of WMC group, target flicker frequency, stimulus congruency, and single-trial SSVEP amplitude for target and flankers (averaged over stimulus-to-response window, no baseline correction applied) and interactions between the fixed factors. A random intercept term was included to account for participant-specific offsets. The categorical factors, such as WMC group (low and high), stimulus congruency (incongruent and congruent), and target flicker frequency (12.5 and 10 Hz) were dummy-coded to 0 and 1 (e.g., low-WMC was 0 and high-WMC was 1) before being entered in the models as fixed effects. Next, a model simplification procedure was performed by iterative removal of non-significant fixed effects and interactions while ensuring a stable goodness of the model fit by log-likelihood-based model comparison using χ^2 statistics (Baayen, Davidson, & Bates, 2008). We also examined whether the effect of target flicker frequency (10 or 12.5 Hz) had a different effect on the RTs of each participant. For this we included a random slope for target flicker frequency per participant, and compared if this improved the model fit. Following previous

reports on positive relationship between RT and response-locked theta power (Cohen & Cavanagh, 2011a; Cohen & van Gaal, 2014) we also included in the model single-trial response-locked theta power (no baseline correction applied, averaged over -200 to 100 ms window) as an additional factor.

Results

Behavioral performance. Despite the presence of the flicker, a typical congruency effect was observed (Figure 3.2). Responses were faster ($F(1,31) = 35.48$, $p < .001$, $\eta^2_p = .53$) and more accurate ($F(1,31) = 7.49$, $p = .01$, $\eta^2_p = .20$) on congruent (510 ms; 7.2% error rate) than on incongruent trials (518 ms; 8.1% error rate). Consistent with previous reports (Heitz & Engle, 2007; Keye et al., 2009; Wilhelm et al., 2013), no statistically significant differences in reaction times (RTs) between high- and low-WMC individuals were observed ($F(1,31) = 0.78$, $p = .383$, $\eta^2_p = .03$). High-WMC individuals were numerically faster, and significantly less accurate ($F(1,31) = 8.10$, $p = .008$, $\eta^2_p = .207$). A follow-up analysis revealed that group differences in accuracy reflected that high-WMC individuals attained the instructed 90% accuracy requirement (one-sample t-test of error rate against 10 %: $t(16) = 0.72$, $p = .481$), whereas low-WMC did not ($t(15) = 5.86$, $p < .001$).

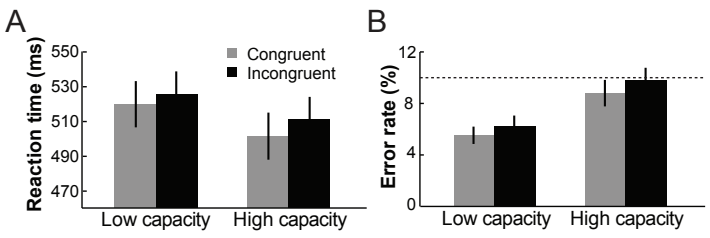

Figure 3.2. Behavioral results. Bars show reaction time (A) and error rate (B) as a function of working memory capacity. The error bars reflect one standard error of the mean. Dashed line in (B) denotes 10% error rate (the instructed performance level).

The size of the interference effects (measured as RT and accuracy differences on incongruent vs. congruent trials) did not differ between groups (RT: $t(31) = 1.38$, $p = .177$; accuracy: $t(31) = 0.41$, $p = .684$), corroborating previous findings when proportions of congruent and incongruent trials were kept equal (Heitz & Engle, 2007; Keye et al., 2009; Wilhelm et al., 2013). Because conventional ANOVAs do not allow for inferences supporting the null hypothesis (Gallistel, 2009), we performed a Bayesian ANOVA so that the strength of evidence in favor of the absence of an effect of WMC group could be evaluated (Rouder et al., 2012). We compared Bayes factors from a model including the main effect of congruency only with a full model including main effects of WMC group and congruency and their interaction. The evidence against including an interaction and the main effect of WMC in the reaction time ANOVA model was 75:1, clearly indicating that groups did not differ in reaction time.

WMC-related differences in attention control. SSVEP amplitudes showed typical attention-related SSVEP effects when collapsing across both groups (Toffanin et al., 2009; Muller et al., 2003), such that SSVEP amplitudes were higher for the targets than for the flankers

both for 10 Hz and for 12.5 Hz tagging frequencies (Figure 3.1B). Furthermore, the topographical distribution of SSVEPs elicited by the flickering stimuli showed a maximum response at central occipitoparietal electrodes for the target, and at lateral electrodes for the flankers (Figure 3.3A). Having demonstrated a typical attentional modulation of SSVEP amplitude, we further analyzed changes in SSVEP amplitude over time.

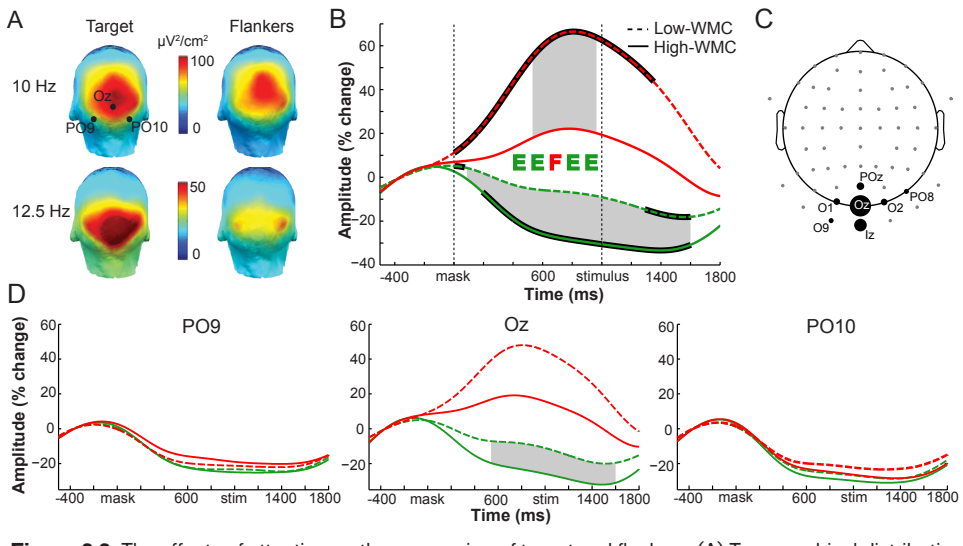

Figure 3.3. The effects of attention on the processing of target and flankers. (A) Topographical distribution of SSVEP power values ($\mu V^2/cm^2$) estimated by FFT of the data in the time window 0 to 1600 time-locked to the pre-stimulus mask onset. Plotted separately for target and flanker stimuli flickering at 10 and 12.5 Hz. (B) The time-course of SSVEP amplitudes for the target (red lines) and flankers (green lines) at the subject-specific best-electrode, averaged over two frequency-tagging conditions (10 Hz target and 12.5 Hz target, flankers tagged with 12.5 and 10 Hz respectively). Grey areas represent statistically significant differences between high- and low-WMC groups (corrected for multiple comparisons using cluster-based permutation testing), and black bolded lines represent statistically significant differences relative to the baseline (corrected for multiple comparisons using cluster-based permutation testing). (C) The distribution of electrodes used as a subject-specific "best-electrode" for SSVEP analysis. The size of the black circles indicates the relative frequency of the electrode used across participants: Oz (N = 15), Iz (N = 9), POz (N = 3); O1 (N = 2), O2 (N = 2), PO8 (N = 1), O9 (N = 1). (D) The time-course of SSVEP amplitudes for the targets and flankers at occipital electrodes (PO9, Oz, and PO10), demonstrating that group differences in the SSVEP amplitudes were observed only at occipital electrodes that showed strong SSVEP but were absent at electrodes that showed no clear SSVEPs (A).

For both WMC groups, SSVEPs elicited by the central hash mark of the mask (i.e., the target position) showed an increase in amplitude relative to the pre-mask baseline period (-500 to -200 ms), an effect that was mirrored by a decrease in the amplitude for the flanking hash marks (Figure 3.3B). These SSVEP amplitude differences during the pre-stimulus mask period continued into the stimulus presentation time. This pattern of results suggests that participants were focusing attention on the spatial location of the central item before and during the actual presentation of the target stimulus.

The high- relative to the low-WMC group showed a significantly larger decrease in SSVEP amplitude for the flanking stimuli (all p values < .05 in the time interval 90 ms to 1600 ms after the mask onset, corrected for multiple comparisons using cluster-based permutation testing), whereas the low- relative to high-WMC group exhibited a stronger enhancement for the central stimulus (all p values < .05 in the time interval 540 ms to 970 ms after pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing). Comparison of SSVEP amplitudes against the baseline revealed the amplitude of the target was significantly enhanced in the low-WMC group (all p values < .05 in the time interval 0 ms to 1350 ms after pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing), whereas target SSVEP amplitude did not significantly differ from the baseline for the high-WMC group (Figure 3.3B). However, high-WMC individuals showed suppression of the flanking stimuli both during the pre-stimulus mask and stimulus presentation periods (all p values < .0125 in the interval 190 ms to 1600 ms after the pre-stimulus mask onset, corrected for multiple comparisons using cluster-based permutation testing). For the low-WMC group, flanker suppression was significant only during the imperative stimulus presentation time (1290 ms to 1600 ms).

Together these results show that although both low- and high-WMC groups attained relatively increased attention to targets compared to flankers, the groups used different strategies to obtain this signal-to-noise ratio: The low-WMC group increased attention to the target whereas the high-WMC group suppressed attention to the flankers.

Control analyses for SSVEP effects. Individual differences in endogenous task-related upper alpha suppression have been previously reported in studies comparing performance of high- and low-IQ individuals (Doppelmayr et al., 2005; but see Toffanin et al., 2007). To ensure that group differences in SSVEP amplitudes were not simply due to differences in upper alpha power, we conducted a series of additional analyses.

Although both groups showed topographically widespread upper alpha power suppression during the pre-stimulus mask and stimulus presentation (Figure 3.4A), group differences in alpha were not statistically significant (all p values >.05 in the interval of interest from 0 ms to 1600 ms after the mask onset, corrected for multiple comparisons using cluster-based permutation testing; Figure 3.4B). To quantify support for the null hypothesis, we compared Bayes factors from a model including WMC group as a fixed effect and a random effect of participant identity with a model including a random effect of participant identity only. Single-trial alpha power in a 0-1000 ms time window (no baseline correction applied) averaged over Oz, POz, and Cz electrodes was used as a dependent variable. The evidence in favor of including WMC group was 0.4:1, which slightly favors excluding this factor altogether, suggesting that any WMC-related differences in alpha power are negligible for the observed group differences in SSVEP amplitudes.

Moreover, statistically significant group differences in SSVEP amplitudes were constrained to occipital electrodes that showed strong SSVEPs (Figure 3.3D); electrodes that showed no clear SSVEPs also showed no group differences, thus further supporting the interpretation that the changes in SSVEP amplitudes reported here reflect group differences in attention control rather than differences in alpha suppression.

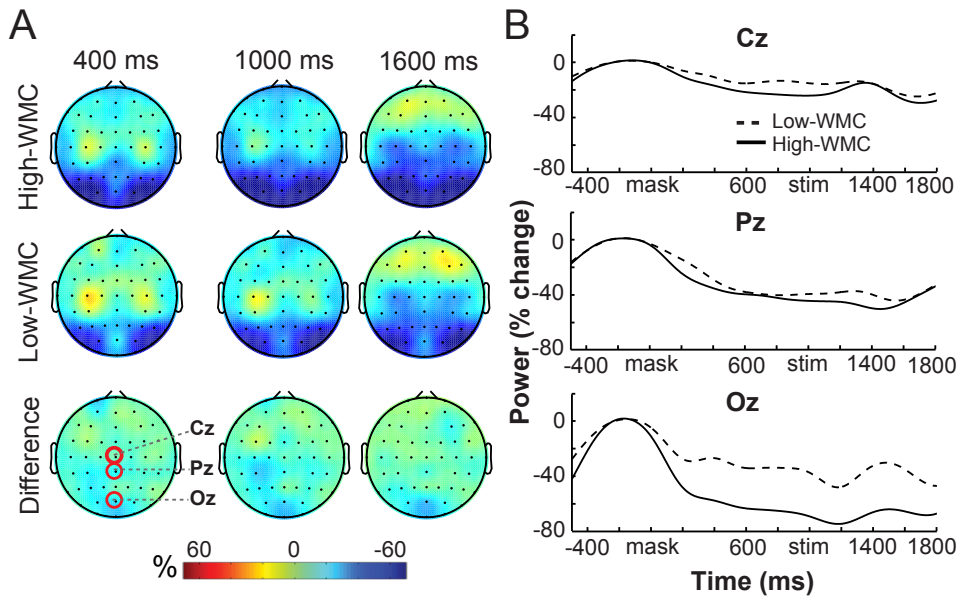

Figure 3.4. Topographical maps and the time-course of upper-alpha (10-13.5 Hz) power. (A) Each topographical map represents activity from the time point indicated in the graph ± 200 ms. (B) The time course of upper-alpha changes in power relative to the baseline period (-300 to -100 ms) in three scalp locations (Cz, Pz, and Oz). These data demonstrate that differences between high- and low-WMC individuals in SSVEPs were not due to differences in widespread endogenous alpha over occipital/parietal regions.

Conflict-related theta-band power. Theta-band power was increased compared to the baseline period in frontocentral sites for all conditions, with a spatial peak at the FCz electrode (Figure 3.5A, C). Consistent with previous reports (Cavanagh et al., 2009; Nigbur et al., 2012), theta-band power was increased more for incongruent compared to congruent trials in both stimulus-locked (F (1,31) = 9.60; p = .004, η^2_p = .236) and response-locked (F (1,31) = 8.96; p = .005, η^2_p = .224) analyses. Although conflict-related changes in theta-band activity were evident for both high- and low-WMC individuals (Figure 3.5B, D), no evidence for group differences in conflict processing were observed. The main effect of group was not significant (F < 1; for both stimulus- and response-locked analyses), nor was the Group x Trial type interaction (F < 1; for both stimulus- and response-locked analyses). We further performed a Bayesian ANOVA to compare the evidence in favor of the null hypothesis (a model with the main effect of congruency only) over the alternative (a full model including both main effects and an interaction). Bayes factor analysis showed that a model excluding the main effect of WMC and an interaction with WMC was preferred at least 180:1 in the stimulus-locked analysis, and at least 161:1 in the response-locked analysis, providing strong evidence for absence of differences between high- and low-WMC groups in theta power.

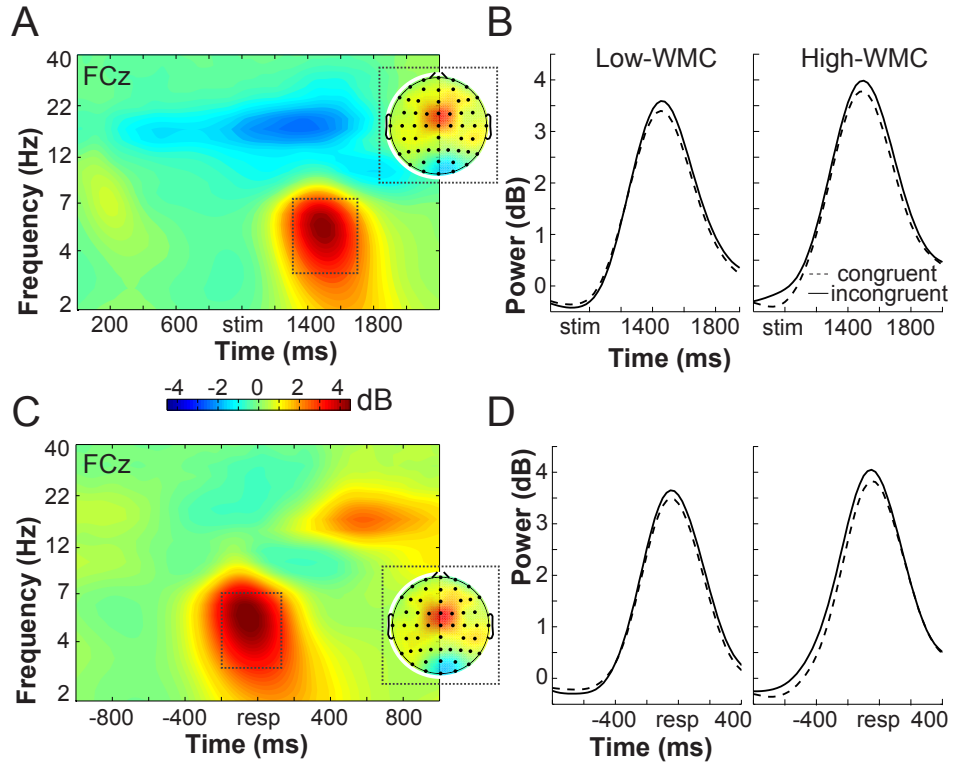

Figure 3.5. Time-frequency representation of a relative theta power (dB). (A) Stimulus-locked and (C) response-locked plots of relative to the baseline period (-300 to -100 ms pre-mask) power at FCz electrode. The inset topographical maps show mean theta-band (3-7 Hz) activity distribution over the scalp in time-frequency windows indicated by dashed squares: 300 to 650 ms for the stimulus-locked and -200 to 100 for the response-locked data. FCz electrode indicated by a black circle. (B) Stimulus-locked and (D) response-locked time-courses of theta-band (3-7 Hz) activity at FCz electrode for congruent and incongruent trials as a function of WMC group.

Single-trial analyses. Although group-level analyses revealed that high- and low-WMC participants differed in attention to the target and flankers, the exact contribution of target enhancement and flanker suppression on single-trial behavioral performance cannot be inferred from group-level results (Pernet, Sajda, & Rousselet, 2011). Therefore, we applied a linear mixed effects (LME) modeling approach to estimate the contribution of experimental parameters (fixed effects) and inter-subject sensitivity to experimental manipulations (random effects) on single-trial log RTs (Pinheiro & Bates, 2000). By means of log-likelihood-based model comparisons (for details see *Methods* section), we derived a best-fitting model. Specifications of the model and statistics of the factors are reported in Table 3.1.

Table 3.1. Specifications of the best-fitting LME model and statistics

Fixed effects	β*	**df**	**t-value**	**p-value**
Participant (Intercept)	6.20	36	257	**< .001**
Theta	$1.93*10^{-9}$	16500	18.06	**< .001**
WMC **	$-4.34*10^{-2}$	35	-1.30	.202
Congruency**	$-1.30*10^{-2}$	16470	-5.01	< .001
Target flicker frequency (*Flicker-Target*)**	$1.72*10^{-2}$	35	4.76	**< .001**
Flanker SSVEP amplitude (*SSVEP-Flanker*)	$-2.79*10^{-2}$	5437	-1.51	.132
Theta x WMC **	$5.69*10^{-10}$	16510	3.45	**< .001**
Flanker SSVEP amplitude x WMC **	$5.48*10^{-4}$	3648	2.34	**.019**
Random effects	Variance			
Participant	0.007			
Target flicker frequency (*Flicker-Target*)**	0.0002			

* Unstandardized β values are reported.

** Factors WMC group, stimulus congruency, and target flicker frequency are dummy-coded: Low-WMC = 0, high-WMC = 1, congruent = 1, incongruent = 0, 12.5 Hz = 0, and 10 Hz = 1.

The strongest predictor for log RT was response-locked theta power, such that longer RTs were associated with higher theta-band power (β_{theta}). This effect was stronger for the high-WMC group ($\beta_{theta\ x\ WMC}$). The model also revealed that stronger suppression of the flankers was associated with longer RTs in the high-WMC but not in the low-WMC group ($\beta_{SSVEP\text{-}Flanker\ x\ WMC}$), although factors WMC group (β_{WMC}) and flanker SSVEP amplitude ($\beta_{SSVEP\text{-}Flanker}$) alone did not significantly predict log RTs. Moreover, log RTs were also affected by target flicker frequency ($\beta_{Flicker\text{-}Target}$), such that RTs were significantly slower when the target flickered at 10 Hz than when it flickered at 12.5 Hz. Finally, statistical analysis revealed that LME model with random slopes for target flicker frequency showed a significantly better fit compared to the model that included only random intercepts per participant (χ^2 (12) = 10.22, $p < .01$), meaning that there were individual differences in sensitivity to the flicker frequency.

Discussion

This study provides direct electrophysiological evidence that WMC is related to the control of attention to both relevant and irrelevant information (Sauseng et al., 2009). In contrast to previous experimental designs that tested responses to relevant and irrelevant information in separate trials (Fukuda & Vogel, 2009, 2011; Gazzaley et al., 2008), we used an experimental approach that allowed us to track attention to relevant and irrelevant information simultaneously within trials. This approach revealed that high-WMC as compared to low-WMC individuals express stronger inhibition of irrelevant information while preparing for the upcoming stimulus, whereas low-WMC individuals enhance the relevant information more, possibly to compensate for deficient distractor suppression. Single-trial analyses showed that behavioral performance was predicted by trial-to-trial fluctuations in distractor suppression during the stimulus-response period for high-, but not for low-WMC participants. Taken together, these findings suggest that the ability to suppress irrelevant information is the key underlying neural mechanism by which superior attentional control abilities are implemented. Importantly, as average behavioral performance was similar for the two groups, the differences in neural dynamics reported here cannot be attributed to group differences in behavioral performance.

These individual strategic differences not only clarify the mechanisms behind more proficient attentional control often exhibited by high-WMC individuals (Kane & Engle, 2003; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), but also suggest an explanation for the weak or non-existent relationship between WMC and behavioral performance in some attention-demanding tasks that challenge attention control abilities (e.g., Heitz & Engle, 2007; Keye et al., 2009; Morey et al., 2012; Wilhelm et al., 2013). Namely, although individual differences in control of attention affect performance in WMC tasks, they will not necessarily translate into differences in performance in other attention-demanding tasks, because inefficient suppression of irrelevant information can be countered by an attentional boost to relevant information. Thus, it appears that the same signal-to-noise ratio can be achieved either by suppressing distractors or by enhancing targets. These two strategies appear able to result in similar performance, yet enhancement of targets is likely to be less neurally efficient (Neubauer & Fink, 2009).

In addition to revealing WMC-related differences in the temporal dynamics of attention control, our findings provide new insights into the relationship between the availability of working memory resources and dispersion of the "Mexican-hat" shaped distribution of spatial attention (Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005). Specifically, earlier work has shown that alternating zones of attentional facilitation and suppression are wider in low- than in high-WMC individuals, and even more dispersed after an increase in working memory load (Ahmed & de Fockert, 2012). Our finding of stronger suppression of distractors by high- as compared to low-WMC individuals suggests that efficient suppression may be the mechanism underlying the more focused profile of spatial attention in high-WMC individuals.

In the adaptation of the Eriksen flanker task used in the current study we replicated the conflict-related increase in theta-band power (3-7 Hz) reported in a classical version of the Eriksen flanker task (Cavanagh et al., 2009; Cohen & Cavanagh, 2011b; Nigbur et al., 2012). Single-trial analyses further demonstrated the validity of the current task as a test of cognitive control network function, as reaction times were strongly predicted by trial-to-trial fluctuations in theta power (Cohen & Cavanagh, 2011b). However, although previous reports of WMC-related differences in connectivity between DLPFC and other parts of the frontal cognitive control network (Cole et al., 2012; Faraco et al., 2011) might lead one to expect a relation between WMC and frontal midline theta, we did not find such differences. To our knowledge, the only other study to use EEG to examine WMC-related differences in conflict processing found group differences only in post-error brain activity (Miller, Watson, & Strayer, 2012). The failure to find group differences in theta power might also be related to

the relatively long (1-s) foreperiod used in this experiment. Having a foreperiod might have resulted in similar priming of task-related functional brain regions for both WMC groups (Fassbender, Foxe, & Garavan, 2006), thereby resulting in similar levels of conflict and absence of group differences in theta power.

The findings that high- and low-WMC individuals use different strategies to deal with distracting information have implications for attempts to use working memory training to increase general cognitive and intellectual abilities (Slagter, 2012). Specifically, our results suggest that training tasks that foster the cognitive process of inhibiting irrelevant information (Buschkuehl, Jaeggi, & Jonides, 2012) would be more beneficial than tasks that aim for general working memory training.

Finally, our study has more general implications for the study of cognitive processes. Most SSVEP paradigms to date have used long-duration and large stimuli

(e.g., Andersen & Muller, 2010; Muller et al., 2003; Toffanin, de Jong, Johnson, & Martens, 2009), which suggests significant constraint on the types of cognitive processes that can be studied with SSVEP. In contrast, our finding of attentional modulation of a single target flanked by four salient distractors demonstrates that SSVEPs can be successfully applied to a variety of cognitive tasks, even those with small stimuli and relatively short presentation times.

To conclude, by simultaneously and independently measuring attention to the targets and distractors in a conflict task we reveal that high- and low-WMC individuals use different strategies to filter out distracting information. Specifically, high-WMC individuals focus on suppressing irrelevant information, whereas low-WMC individuals focus on enhancing relevant information. Because complex span tasks show high test-retest reliability (Engle, 2010; Unsworth et al., 2005), these strategic differences between high- and low-WMC individuals likely reflect stable trait-like mechanisms that affect perceptual processing of irrelevant information.

4 Brain networks underlying WMC-related differences in cognitive control

Executive-attention theory proposes a close relationship between working memory capacity (WMC) and cognitive control abilities. However, conflicting results are documented in the literature, with some studies reporting that individual variations in WMC predict differences in cognitive control and trial-to-trial control adjustments (operationalized by the size of congruency effect and congruency sequence effects), while others report no WMC-related differences. It is possible that these discrepancies are due to low sensitivity of behavioral measures. We hypothesized that brain network dynamics might be a more sensitive measure. Thus, in the present study, we measured human EEG during the Simon task to characterize WMC-related differences in the neural dynamics of conflict processing and adaptation to conflict. Although high- and low-WMC individuals did not differ behaviorally, there were substantial WMC-related differences in theta (4-8 Hz) and delta (1-3 Hz) connectivity in fronto-parietal networks. However, WMC-related differences in local theta and delta power were less pronounced. These results suggest that the relationship between WMC and cognitive control abilities is more strongly reflected in large-scale oscillatory network dynamics than in spatially localized activity or in behavioral task performance.

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Fronto-parietal network oscillations reveal relationship between working memory capacity and cognitive control

Introduction

Balancing automatic and controlled behavior is necessary for fast and accurate performance. Insufficient levels of control can lead to errors (Rabbitt & Rodgers, 1977), whereas excessive control slows down responses (Danielmeier & Ullsperger, 2011) or even impairs skilled performance (Wulf, 2007). Fluctuations in the levels of control are evident in trial-to-trial changes in reaction time (RT) and accuracy in response-conflict tasks (Eichele, Juvodden, Ullsperger, & Eichele, 2010), in which task-relevant and task-irrelevant stimulus features prime conflicting responses (Egner, 2008).

The executive-attention theory of working memory capacity (WMC) proposes that high- compared to low-WMC individuals are better at controlling attention, resulting in more stable representations of stimulus-response mappings and less interference from task-irrelevant information (Kane et al., 2007; Kane & Engle, 2003). Although congruency effects (the performance difference between incongruent and congruent trials) can be larger for low- compared to high-WMC individuals (Kane & Engle, 2003; Weldon et al., 2013), this effect seems to depend on the task and contextual factors such as the ratio of congruent and incongruent trials (Heitz & Engle, 2007; Kane & Engle, 2003; Keye et al., 2009; Morey et al., 2012; Weldon et al., 2013). Similarly, WMC-related differences in trial-to-trial cognitive control adjustments reflected in congruency sequence effects are inconclusive (Hutchison, 2011; Keye et al., 2013; Keye et al., 2009; Meier & Kane, 2012; Weldon et al., 2013). However, EEG signatures of performance monitoring (e.g. error-related negativity) might be more sensitive to WMC-related differences in cognitive control compared to behavioral measures (Miller et al., 2012).

fMRI findings suggest that fronto-parietal network connectivity might be relevant for individual differences in both WMC and cognitive control abilities (Cole et al., 2012; Edin et al., 2009; Faraco et al., 2011). However, changes in functional connectivity at behaviorally relevant timescales might be missed by fMRI, and cannot be measured with event-related potentials (Cohen, 2011b). In contrast, synchronous oscillations between neuronal ensembles have been proposed to be a mechanism for inter-areal communication (Buzsaki & Draguhn, 2004; Fries, 2005), and can be measured with EEG/MEG data using time-frequency analysis techniques.

Therefore, the purpose of the present study was to test whether oscillatory fronto-parietal network dynamics is a sensitive marker of WMC differences (as measured by complex span tasks; Redick et al., 2012) in cognitive control. We recorded EEG while subjects performed a Simon task, in which incongruence between the task-relevant stimulus feature (color) and the task-irrelevant feature (location) elicits response conflict. We focused on theta (4-8 Hz) oscillatory activity over medial frontal cortex (MFC), which is associated with cognitive control processes (Cavanagh et al., 2009; Cohen & Ridderinkhof, 2013; Hanslmayr et al., 2008; Nigbur et al., 2012). Both theta power over MFC and phase synchronization with lateral prefrontal sites reflects trial-by-trial cognitive control demands and predicts reaction times during response-conflict tasks (Cohen & Cavanagh, 2011a; Cohen & Donner, 2013; Gulbinaite, Johnson, De Jong, Morrey, & van Rijn, submitted). Due to the novelty of our approach, we also characterized the basic oscillatory interactions between MFC and parietal areas during the Simon task.

Method

Participants and WMC screening. Participants were selected from a pool of University of Groningen students who had been tested in the automated versions of the Operation span (OSPAN) and the Symmetry span tasks (Redick et al., 2012) in a separate experimental session at least 5 months prior to the Simon task (N = 618). WMC score for each WMC task was computed using the partial-scoring method (Conway et al., 2005), according to which correctly recalled items are given a partial credit if they are recalled in the correct serial position even though the full list is incompletely recalled. All list lengths were weighted equally and the proportion of correct responses was computed for each list length separately (e.g., 2 of 5 = 0.4, 3 out of 3 = 1.0). Thus obtained proportions were averaged across all lists. Individual WMC scores could range from 0 to 1.

For each individual a composite WMC score was computed by averaging z-transformed scores from both WM tasks. As the goal was to characterize a specific dimension of individual differences rather than to estimate the exact effect size, an extreme group design was used (Yarkoni & Braver, 2010). Participants were invited to an EEG session if a composite WMC score fell in the lower (low-WMC participants) or the upper (high-WMC participants) quartiles of the distribution of composite WMC scores in our database (N = 618, $Q1$ = -0.41, $Q3$ = 0.60).

Participants were 19 high-WMC individuals (z-WMC = 0.97, SD = 0.16) and 20 low-WMC individuals (z-WMC = -1.40, SD = 0.51). Data from 3 participants were excluded due to movement artifacts, 1 due to poor performance, and 1 due to technical problems. Thus, 17 high-WMC (8 females, mean age 21.35, 3 left handed) and 17 low-WMC (15 females, mean age 21.41, 1 left handed) were included in the analysis. All participants had normal or corrected-to-normal vision. The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee. Informed consent was obtained from all participants.

Task. Stimulus presentation and response registration were controlled by custom-written Matlab routines using Psychtoolbox (Brainard, 1997). The stimuli were presented on a 17-inch CRT monitor (1024x768, 100 Hz) at approximately 90 cm viewing distance.

Stimuli for the Simon task were four different color circles, each measuring 2.2 x 2.2 cm (subtending approximately 2° visual angle), presented on a black background 4.5 cm (approximately 5° of visual angle) to the left or right of a white fixation cross. Purple (R: 204 G: 0 B: 204), green (R: 0 G: 104 B: 0), red (R: 204 G: 0 B: 0), and yellow (R: 200 G: 200 B: 0) colors were used, with two stimuli mapped onto each hand. Half of the participants responded to purple and green circle by pressing the "x" key with the left index finger, and to the red and yellow circle by pressing the ">" key with the right index finger; the other half of the participants used the opposite mapping. Each trial began with the presentation of a stimulus to the right or to the left of the fixation cross that remained in view until a response was made or a deadline of 1500 ms was exceeded. After a response was made, a fixation cross was presented for 1000 ms (Figure 4.1).

The overall probabilities of congruent and incongruent trials, trial-to-trial congruency transitions (congruent-congruent, cC; congruent-incongruent, cI; incongruent-congruent, iC; incongruent-incongruent, iI), and the proportions of left- and right-hand responses were kept equal. Due to possible response priming effects on the size of the congruency sequence effects (Mayr, Awh, & Laurey, 2003), a pseudo-random sequence of stimuli was designed to contain no exact stimulus-response repetitions.

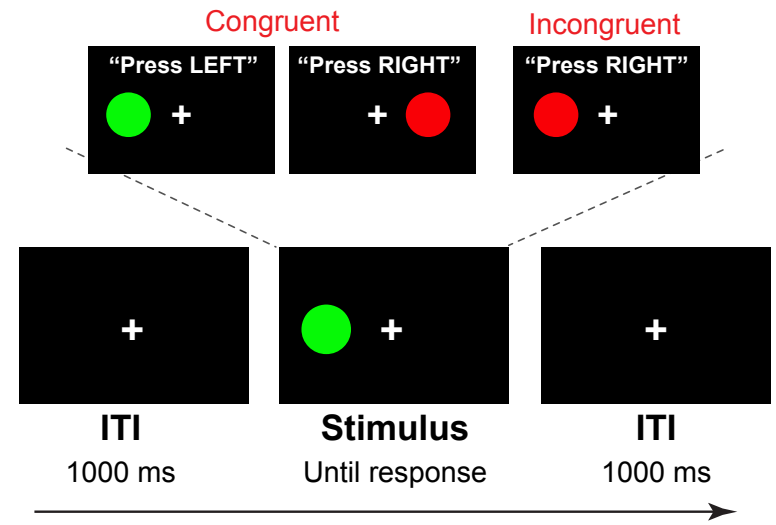

Figure 4.1. Trial structure and stimuli. A four-alternative Simon task, in which two colors are mapped on the left, and two on the right hand (counterbalanced across participants). On each trial one of the four stimuli is shown in the location spatially congruent or incongruent with the response hand. In this example, congruent stimulus is presented.

Procedure. Participants were tested individually in a dimly lit room. They were instructed to respond as quickly as possible while maintaining an accuracy of at least 90%. This was done to avoid ceiling effects in performance and minimize the effect of individual differences in speed-accuracy tradeoff settings. The task consisted of 70 practice trials and 1024 experimental trials. For the first 10 practice trials, feedback was given after each trial; the remaining 60 practice trials were divided into three blocks of 20 trials each with feedback (mean RT and accuracy) provided after each block. Experimental trials were divided in eight blocks of 64 trials each, with feedback provided at the end of each block.

EEG recording and preprocessing. Scalp EEG was recorded using 62 tin electrodes (Electro-cap International Inc., Eaton, Ohio, USA) positioned according to a modified version of the international 10-10 system (6 additional electrodes were placed 10% below standard FT7, PO7, O1, FT8, PO8, and O2 electrode positions; F1, F2, CP1, CP2, FT7, and FT8 were not measured). Two additional reference electrodes were placed on the mastoids. Vertical and horizontal eye movements were recorded using four additional electrodes, two of which were placed below and above the left eye and the other two on the outer eye canthi. The data were recorded using the "REFA 8–72" amplifier (Twente Medical Systems, Enschede, The Netherlands), digitally low-pass filtered at 140 Hz and sampled at 500 Hz. All offline data preprocessing and analysis was done using EEGLAB toolbox for Matlab (sccn.ucsd.edu/eeglab/) and custom written Matlab scripts (Cohen, 2014).

The data were re-referenced offline to the average activity recorded at the mastoids and high-pass filtered at 0.5 Hz. Continuous EEG recording was epoched from -1500 ms to 2000 ms around stimulus onset. Trials containing muscle artifacts or eye blinks during the stimulus presentation period were visually identified and removed. The second artifact

rejection step included independent component analysis (Delorme & Makeig, 2004). Components that did not account for any brain activity, such as eye-movements or noise, were subtracted from the data. Artifact-free data were Laplacian transformed to increase topographical selectivity by filtering-out low spatial frequencies, which are considered to result from volume-conduction. Furthermore, the first trial of each block, error trials (incorrect or no-response trials), post-error trials, anticipatory responses (RTs faster than 150 ms), and trials in which participants pressed both right and left buttons, were excluded from analyses. Error and post-error trials were excluded to isolate neural processes related to conflict processing and conflict adaptation from error-related processing (Cohen & van Gaal, 2014). The average number of trials per condition included in the statistical analysis for both EEG and behavioral data was: 204 (*SD* = 18),182 (*SD* = 22), 185 (*SD* = 20), and 199 (*SD* = 19), for cC, cI, iI, iC trials respectively.

EEG time-frequency analyses. Time-frequency decomposition was performed by convolving stimulus-locked single-trial data from all electrodes with complex Morlet wavelets, defined as:

$$e^{i2\pi f_i t} e^{-t^2/(2\sigma^2)},$$

where t is time, f_i is frequency which ranged from 1 to 40 Hz in 40 logarithmically spaced steps, and σ is the width of each frequency band defined as $n/(2\pi f_i)$, where n is a number of wavelet cycles that varied from 3 to 6 in logarithmically spaced steps to obtain comparable frequency precision at low and high frequencies. Instantaneous power was estimated as the square of the complex convolution signal z (*power* = real[z(t)]^2 + imag[z(t)]^2) and averaged across trials. Power values at each time-frequency point were normalized by converting to the decibel scale to account for power-law scaling of oscillations in different frequency bands (amplitude increases when frequency decreases) by using the formula:

$$10\log_{10}(power/baseline),$$

where power from -400 to -100 ms pre-stimulus period served as the frequency band-specific baseline.

The phase angle φ_t = arctan (imag[z(t)]/real[z(t)]) of the complex convolution result was used to compute frequency-band specific inter-site phase clustering (ISPC), a measure of functional connectivity between the brain areas (Buzsaki & Draguhn, 2004; Fries, 2005). ISPC is defined as trial-average phase angle difference between two electrodes j and k at each time-frequency point:

$$\left|\frac{1}{n}\sum_{t=1}^{n} e^{i(\varphi_{jt}-\varphi_{kt})}\right|,$$

where n is trial count. Many previous studies have demonstrated that applying the Laplacian to scalp EEG data renders them appropriate for connectivity analyses (Cohen & Cavanagh, 2011a; Nigbur et al., 2012; Srinivasan, Winter, Ding, & Nunez, 2007).

Statistical analyses. Statistical analyses were based on previous research-informed and data-driven approaches. Previous studies have consistently demonstrated that WMC-related differences in cognitive control are driven by differences on post-incongruent trials (smaller conflict effects after incongruent trials; Gulbinaite & Johnson, 2013; Keye et al., 2009; Weldon et al., 2013), with modest or no WMC-related differences in post-congruent trial conflict effects. Therefore, we tested WMC-related differences on post-incongruent trials only.

Behavioral data. Two sets of ANOVAs were performed. First, the general task effects (collapsing over groups) were evaluated by submitting mean RTs and percentage error to separate repeated-measures ANOVAs with current trial type (congruent and incongruent) and previous trial type (congruent and incongruent) as within-subject factors. Second, WMC effects on conflict adaptation were evaluated in another set of mixed ANOVAs with post-incongruent trial type (congruent iC, and incongruent iI) as within-subject factor, and WMC group (high and low) as between-subject factor.

EEG data. Previous studies showed early conflict-related modulations of activity in parietal areas, followed by the later occurring modulations in fronto-central areas (Cohen & Ridderinkhof, 2013; Schiff, Bardi, Basso, & Mapelli, 2011; Sturmer et al., 2002). Based on these findings, we adopted the following procedure. First, we created topographical plots for power in the theta (4-8 Hz) frequency band in early (50-300 ms) and late (300-550 ms) time windows, time-locked to the stimulus onset and averaged over all trials. Second, electrodes that showed the largest change in condition- and group-averaged power in either the early or the late time window were selected. Third, subject- and condition-averaged time-frequency power plots were constructed for these electrodes. Fourth, time-frequency windows with the largest power increase were selected based on visual inspection (marked in Figures 4.3, 4.4, 4.5 as dashed squares in time-frequency plots), and within this window, the subject-specific time-frequency point with maximum power was found. Note that this selection procedure is orthogonal to any WMC group- or condition-specific differences in power, and therefore could not introduce any biases into the results. Finally, for each subject, the condition-specific power surrounding 100 ms of the peak time-frequency point was used for statistical analyses. This approach was chosen to preserve subject-specific peak frequency activity (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014), which may be correlated with WMC (Moran et al., 2010). For ISPC analyses, the same analysis steps were followed. Group-level statistics were performed using the same procedure that we used for the behavioral data.

Results

Behavioral results. Behavioral results are illustrated in Figure 4.2. Overall RTs on congruent compared to incongruent trials were faster (477 ms vs. 485 ms; $F(1, 32) = 20.81$, $p < .001$, $\eta^2_p = .39$) and slightly more accurate (7.6% vs. 8.9% error-rate; $F(1, 32) = 3.54$, $p = .069$, $\eta^2_p = .10$). A current by previous trial type interaction reflected the typical Simon task congruency sequence effects: Positive conflict effect (Simon effect) after congruent trials and a reverse Simon effect after incongruent trials (RTs: $F(1, 32) = 70.36$, $p < .001$, $\eta^2_p = .68$; error-rate: $F(1, 32) = 83.76$, $p < .001$, $\eta^2_p = .72$; Figure 4.2A, right panel). Although group differences in

the conflict effect following incongruent trials were in the predicted direction (larger reverse Simon effect for low- compared to high-WMC group; Figure 4.2B), WMC x Post-incongruent trial type interaction was not significant ($F(1, 32) = 2.71$, $p = .110$, $\eta^2_p = .08$).

EEG results. In general, task-related increases in theta-band power compared to the baseline period were observed over stimulus-contralateral posterior parietal areas (spatial peaks around PO8 and PO7, Figure 4.3A) in the earlier time window (50-300 ms post-stimulus), and over midfrontal areas (centered around FCz) in the later time window (300 – 550 ms post-stimulus; Figure 4.3A). Task-related changes in the delta-band (1-3 Hz; Figure 4.5A1) were pronounced in a 200-600 ms time window over stimulus-contralateral anterior parietal sites (spatial peaks around P3 and P4). We therefore focused our analyses on these time-frequency-electrode regions-of-interest in the power analyses.

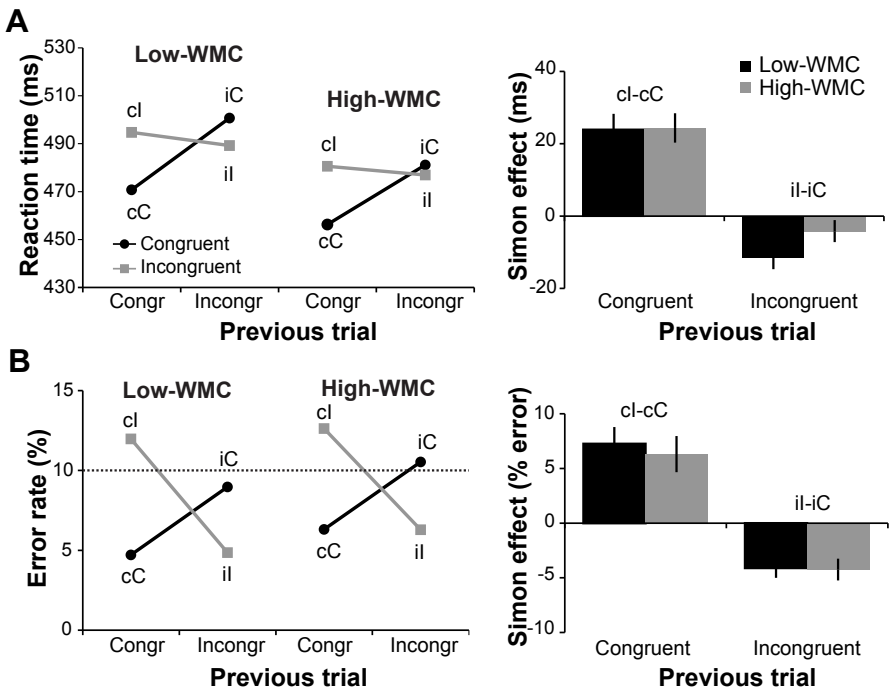

Figure 4.2. Behavioral results. Left-side panels depict RTs (A) and error rates (B) as a function of current and previous trial type, and working memory capacity group. Right-side panels represent post-congruent and post-incongruent trial conflict effects: RT and error rate differences between incongruent and congruent trials. The error bars reflect one standard error of the mean. Dashed line in (B) denotes 10% error rate (the instructed minimum performance level).

Parietal theta power. Stimulus-contralateral parietal theta power was stronger for congruency repetitions (cC and iI) than for congruency alternations (cI and iC), as indicated by a current and previous trial type interaction ($F(1, 32) = 7.37$, $p = .010$, $\eta^2_p = .18$; Figure 4.3B2). High- and low-WMC groups differed in post-incongruent conflict effects ($F(1, 32) = 4.30$, $p = .046$, $\eta^2_p = .12$), such that low-WMC individuals showed a conflict effect ($t(16) = 3.09$, $p = .007$), whereas high-WMC individuals did not ($t(16) = 0.48$, $p = .637$). Together these results show that processing of spatial stimulus features in posterior parietal cortex was modulated by conflict and by WMC.

Midfrontal theta power. Replicating previous findings (Cohen & Ridderinkhof, 2013; Nigbur, Ivanova, & Sturmer, 2011), incongruent trials as compared to congruent trials elicited a stronger increase in theta power at FCz ($F(1, 32) = 19.23$, $p < .001$, $\eta^2_p = .37$). There was also significant current and previous trial type interaction ($F(1, 32) = 79.18$, $p < .001$, $\eta^2_p = .71$; Figure 4.3C2), reflecting adaptation to the previous trial conflict. However, there were no group differences in cognitive control adjustments in response to conflict, as reflected by non-significant WMC and post-incongruent trial type interaction ($F(1, 32) = 1.39$, $p = .248$, $\eta^2_p = .04$; Figure 4.3C2).

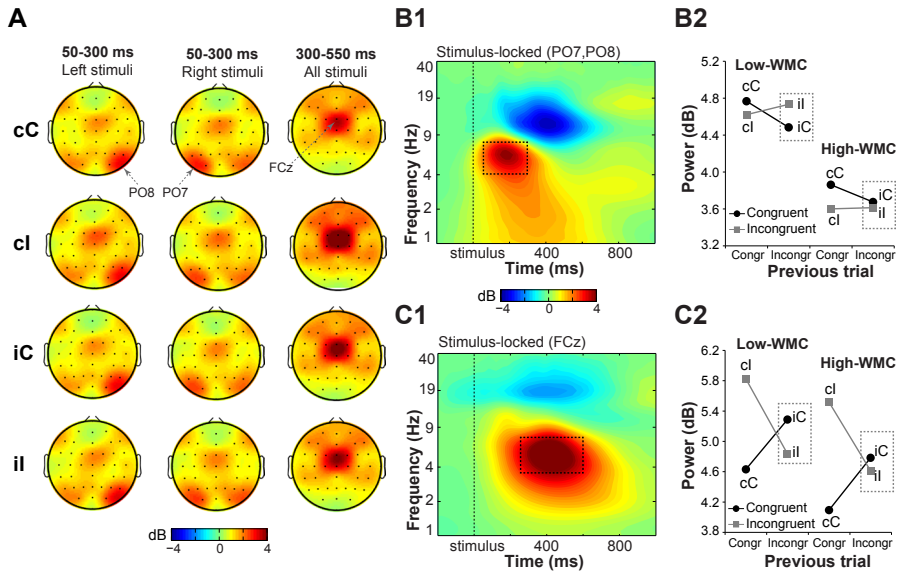

Figure 4.3. Task-related changes in theta power. (A) Topographical maps of power in the theta band (4-8 Hz) averaged over early (50-300 ms) and late (300-550 ms) intervals, separated for previous and current trial type (lowercase and uppercase letters respectively). Left- and right-hemifield stimulus trials are shown separately to emphasize laterality effects observed over parietal electrodes. (B1) Condition-averaged changes in power relative to the baseline (-400 – -100 ms) period over parietal electrodes contralateral to stimulus presentation hemifield (averaged PO8 and PO7); (C1) and over medial frontal electrode FCz. Dashed squares represent the time-frequency windows used for the ANOVAs. Condition-specific changes in theta power over parietal (B2) and medial frontal areas (C2) as a function of previous and current trial type, and WMC group. Dashed squares represent conditions used for WMC-related analyses.

Fronto-parietal theta ISPC. Visual inspection of condition- and group-averaged ISPC data between FCz (the "seed") and parietal areas revealed increases in theta-band connectivity relative to the baseline in: (1) the early time-frequency window (50-250 ms) over stimulus-ipsilateral posterior parietal sites (spatial peaks around PO7 and PO8 electrodes; Figure

4.4A1), (2) the later time-frequency window (150-350 ms) over stimulus-contralateral anterior parietal sites (spatial peaks around P3, P4, P5, P6 electrodes; Figure 4.4B1), (3) and the late time-frequency window (300-600 ms) in anterior parietal sites bilaterally (spatial peaks around P3, CP5, P4, CP6, Figure 4.4C1). These time-frequency-electrode windows were used as regions-of-interest in the ISPC analyses.

FCz-stimulus-ipsilateral parietal ISPC in the early time-frequency window (50-300 ms; Figure 4.4A2) was not modulated by current or previous trial type (*p*'s from .182 to .283), nor were there group differences on post-incongruent conflict effects ($F(1, 32) = 2.53$, $p = .122$, $\eta^2_p = .07$; Figure 4.4A3).

Analysis of FCz-stimulus-contralateral parietal ISPC in the later time-frequency window (150-350 ms; Figure 4.4B2) revealed WMC-related differences in adaptation to the previous trial conflict as indicated by significant WMC group x Post-incongruent trial type interaction ($F(1, 32) = 7.85$, $p = .009$, $\eta^2_p = .20$). Decomposition of this interaction revealed stronger ISPC on incongruent (iI) vs congruent (iC) trials for the low-WMC group ($t(16) = 3.01$, $p = .008$), with no effect of trial type for the high-WMC group ($t(16) = 1.24$, $p = .235$).

Finally, ISPC between FCz and anterior parietal areas in the late time-frequency window (300-600 ms; Figure 4.4C2) was stronger for incongruent than for congruent trials ($F(1, 32) = 9.69$, $p = .004$, $\eta^2_p = .23$), replicating similar findings in the Eriksen flanker task (Nigbur et al., 2012). The Current trial type x Previous trial type interaction was also significant ($F(1, 32) = 21.69$, $p < .001$, $\eta^2_p = .40$), reflecting typical congruency sequence effects (Figure 4.4C3). No other effects or interactions reached criteria for statistical significance.

Midfrontal-to-lateral-frontal theta ISPC. ISPC between FCz and lateral prefrontal sites (electrodes AF3, AF4, F6, and F5) was evaluated in the same 300-550 ms time window used in theta power analyses (Figure 4.4C4). There was a main effect of current trial type, with stronger connectivity between FCz and lateral prefrontal areas during incongruent vs. congruent trials ($F(1, 32) = 14.37$, $p < .001$, $\eta^2_p = .30$). The significant interaction between current and previous trial type indicated that ISPC between FCz and lateral prefrontal sites was modulated by the level of conflict on the previous trial ($F(1, 32) = 46.29$, $p < .001$, $\eta^2_p = .58$;).

There was also a significant interaction between WMC group and post-incongruent trial type ($F(1, 32) = 5.13$, $p = .03$, $\eta^2_p = .14$). Follow-up analyses showed that ISPC was stronger on congruent (iC) than on incongruent (iI) trials for the low-WMC group ($t(16) = 3.58$, $p = .002$), whereas for the high-WMC group the effect of trial type was not significant ($t(16) = 0.45$, $p = .663$; Figure 4.4C5).

Taken together, these ISPC analyses revealed that the configuration of conflict-related fronto-parietal networks shifted over time: First ISPC was increased between frontal and stimulus-ipsilateral posterior parietal areas, then between frontal and stimulus-contralateral anterior parietal areas, and finally settled into a bilateral broad fronto-parietal configuration (Figure 4.4A1-C1). Post-conflict adaptation effects in these fronto-parietal network activity patterns were different between the WMC groups already during the early stimulus processing stage (line plots Figure 4.4B2) and continued into the later response-selection stage (line plots Figure 4.4C5).

Parietal delta power and fronto-parietal ISPC. Stimulus-contralateral parietal delta power (Figure 4.5) showed a significant current and previous trial type interaction ($F(1, 32) = 4.95$, $p = .033$, $\eta^2_p = .13$), with a stronger increase in delta power on congruency repetitions (cC,

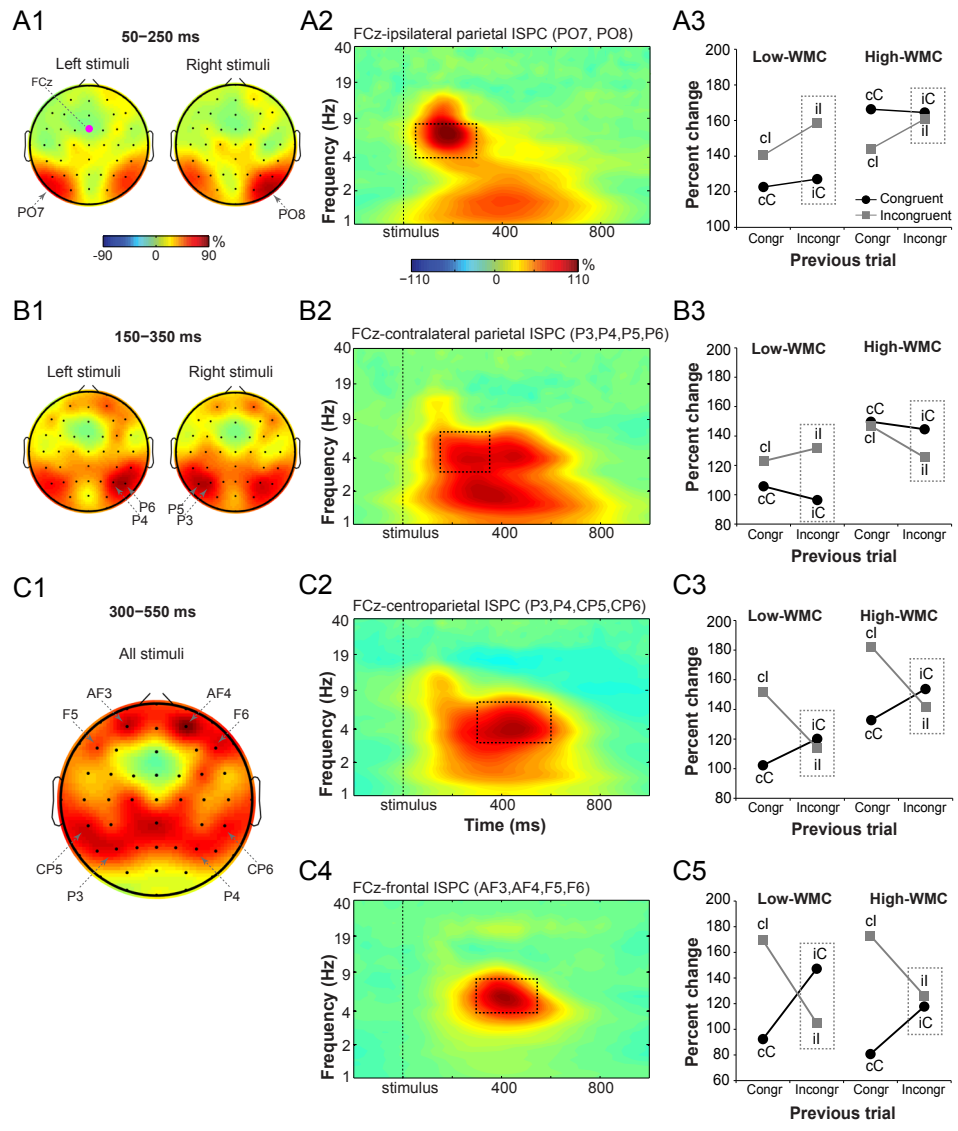

Figure 4.4. Task-related changes in theta inter-site phase clustering. Topographical maps of FCz-seeded ISPC in: (A1) early (50-250 ms), (B1) later (150-350 ms), and (C1) late (300-550 ms) time windows. (A2, B2, C2, C4) Condition- and participant-average time-frequency representation of ISPC between FCz (the "seed") and stimulus-ipsilateral parietal sites (PO7, PO8), stimulus-contralateral parietal sites (P3, P4, P5, P6), bilateral parietal sites (P3, P4, CP5, CP6), and frontal sites (AF3, AF4, F5, and F6). Dashed squares represent the time-frequency windows used for the ANOVAs. (A3, B3, C3, C5) Condition-specific changes in theta-band ISPC as a function of previous and current trial type, and WMC group. Dashed squares represent conditions used for WMC-related analyses.

iI) than on congruency alternations (cI, iC; Figure 4.5A3). There were no group differences on post-incongruent trial conflict effects ($F(1, 32) = 1.38$, $p = .25$, $\eta^2_p = .04$).

Analysis of FCz-seeded ISPC revealed increases in stimulus-contralateral posterior parietal electrodes (spatial peaks around PO7, P08, PO4, PO3; Figure 4.5B1). There was a significant WMC group x Post-incongruent trial type interaction ($F(1, 32) = 6.51$, $p = .016$, $\eta^2_p = .17$; Figure 4.5B3). Decomposition of this interaction showed stronger ISPC on iI vs. iC trials for the low-WMC individuals ($t(16) = 2.22$, $p = .041$), and no effect of the trial type for the high-WMC individuals ($t(16) = 1.63$, $p = .123$).

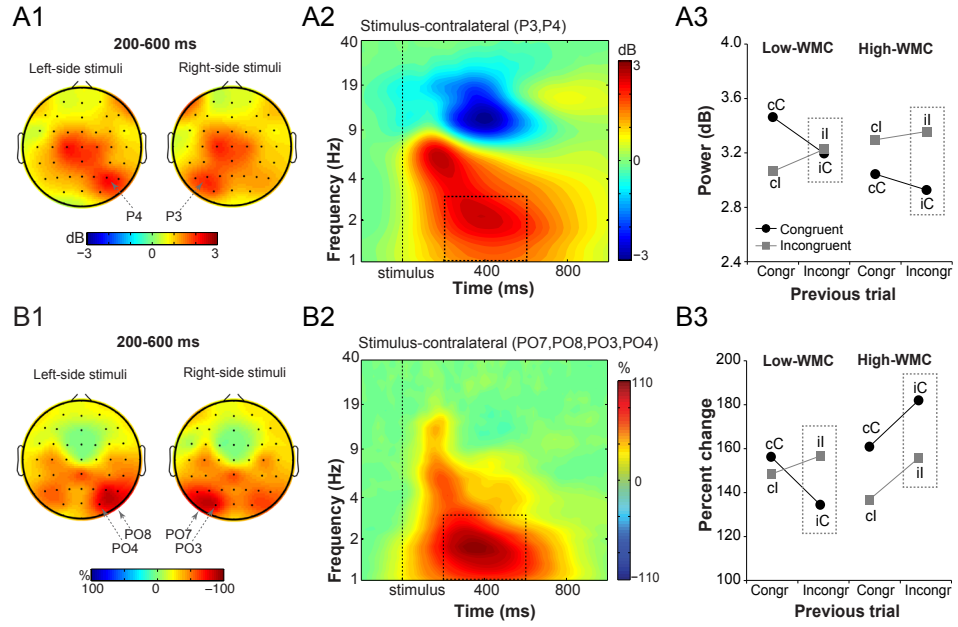

Figure 4.5. Task-related changes in delta power and inter-site phase clustering. (A1) Topographical maps of delta band (1-3 Hz) power and (B1) FCz-seeded ISPC averaged over a 200-600 ms time window. Plotted separately for left- and right-hemifield stimulus trials. (A2, B2) Time-frequency representation of condition-averaged changes in power and ISPC relative to the baseline period (-400 – -100 ms) over stimulus-contralateral parietal electrodes that showed a maximum peak activity (see A1 and B1). Dashed squares represent the time-frequency windows used for the ANOVAs. (A3, B3) Condition-specific changes in power and ISPC as a function of previous and current trial type, and WMC group. Dashed squares represent conditions used for WMC-related analyses.

Discussion

The most striking finding of this study is that the functioning of large-scale networks grouped by oscillatory phase synchronization in theta and delta frequency bands are sensitive markers of WMC-related differences in cognitive control, whereas behavioral task performance did not show statistically significant group differences. This elaborates on the possible neural mechanisms of the executive-attention theory of WMC (Engle & Kane, 2004; Kane et al., 2007), which suggests that high- and low-WMC individuals primarily differ in their ability to control attention. Theta-band oscillatory activity previously has been shown to play a central role within fronto-parietal network communication during attention and cognitive control tasks (Cohen & Ridderinkhof, 2013; Green & McDonald, 2008; Pastotter, Dreisbach, & Bauml, 2013), and has additionally been associated with working memory (Hsieh & Ranganath, 2014; Kahana, Seelig, & Madsen, 2001).

Novel EEG characteristics of the Simon task. In addition to replicating the conflict modulation of midfrontal theta (Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013; Nigbur et al., 2011), we also found an increase in theta activity over stimulus-contralateral areas, likely reflecting processing of the spatial stimulus features (Rusconi, Turatto, & Umilta, 2007; Schiff et al., 2011; Sturmer, Redlich, Irlbacher, & Brandt, 2007). Of novelty is the modulation of early parietal theta-band power by preceding trial context, suggesting that cognitive control mechanisms affect processing of task-relevant and task-irrelevant stimulus features already during the early stimulus processing stages (Appelbaum, Smith, Boehler, Chen, & Woldorff, 2011; Pastotter et al., 2013; Scerif, Worden, Davidson, Seiger, & Casey, 2006; Walsh, Buonocore, Carter, & Mangun, 2011). Opposite to the behavioral results, congruency repetitions were associated with high, and congruency alternations with low, parietal theta power (Figure 4.3B2). A similar pattern in the BOLD signal was observed in the fusiform face area in the face-word Stroop task (Egner & Hirsch, 2005), and in ERPs over parieto-central areas in the Eriksen flanker task (Wendt et al., 2007).

Theta connectivity revealed task-related shifts in fronto-parietal networks along a posterior-anterior axis: From stimulus-ipsilateral posterior parietal areas (50-250 ms) to stimulus-contralateral anterior parietal areas (150-350 ms), and finally to a broad bilateral fronto-parietal network configuration (300-550 ms; Figure 4.4A1-C1). The early stimulus-ipsilateral increase in fronto-parietal connectivity may reflect a fast stimulus-driven involuntary orienting of attention, whereas the later changes in stimulus-contralateral and bilateral connectivity may reflect voluntary reorienting of spatial attention (Corbetta & Shulman, 2002; Sawaki, Geng, & Luck, 2012). Indeed, there are two critical time periods (130-160 ms and 210-240 ms) for spatial attentional orienting (Chambers, Payne, Stokes, & Mattingley, 2004), during which magnetic stimulation of parietal cortex attenuates or abolishes the Simon effect (Schiff et al., 2011).

Although little is known about attention-related lateralization effects in the theta band (Green & McDonald, 2008; Thorpe, D'Zmura, & Srinivasan, 2012), phase synchronization in the alpha band between lower- and higher-level visual regions is increased contralateral to the attended location, whereas alpha amplitude is decreased, reflecting long-range inter-areal communication and inhibitory processes respectively (Doesburg, Green, McDonald, & Ward, 2009; Palva & Palva, 2011). Thus, the observed increase in theta power over stimulus-contralateral parietal areas and early theta synchronization between FCz and stimulus-ispilateral parietal areas, followed by later synchronization between FCz and contralateral-parietal areas, seem to reflect functionally distinct processes.

The novel findings of conflict-related modulation of stimulus-contralateral delta-band power and connectivity highlight that conflict-related modulations occur in frequencies and brain networks beyond midfrontal theta (Cohen & Donner, 2013; Cohen & Ridderinkhof, 2013; Nigbur et al., 2011; Pastotter et al., 2013). Both delta (waking and sleep; Harmony, 2013) and conflict-related theta oscillations originate from medial frontal regions (Agam et

al., 2011; Cohen & Ridderinkhof, 2013). Previously, increased frontal delta-band activity in cognitive control tasks was reported only during errors (Cohen & van Gaal, 2014; Yordanova, Falkenstein, Hohnsbein, & Kolev, 2004). Conflict-modulated delta activity in the present study might be related to delta-band synchronization in the dorsal fronto-parietal network during goal-driven (re)orienting of attention (Daitch et al., 2013).

Group differences in parietal theta- and delta-band activity. Kane and colleagues (Engle & Kane, 2004; Kane et al., 2007; Kane & Engle, 2003) suggested that individual differences in the ability to control attention underlie the often-observed relationship between WMC and performance in response-conflict tasks. Furthermore, they proposed functioning of dorsolateral PFC to be the primary cause for variations in WMC (Kane & Engle, 2002) – theoretical ideas recently supported by several fMRI studies showing WMC-related connectivity differences in fronto-parietal network (Cole et al., 2012; Faraco et al., 2011).

On the behavioral level, consistent with previous reports that kept the proportions of congruent and incongruent trials equal, WMC was related neither to the size of the conflict effect (Gulbinaite & Johnson, 2013; Keye et al., 2013; Keye et al., 2009; Weldon et al., 2013; Wilhelm et al., 2013) nor to the adaptation to the previous trial conflict (Keye et al., 2013). However, WMC-related differences in cognitive control adjustments to the previous trial conflict were evident in theta/delta functional connectivity in fronto-parietal networks.

Group differences in conflict adaption were apparent early in the trial during processing of to-be-ignored location of the stimulus. Following incongruent trials, stimulus-contralateral posterior parietal power and fronto-parietal connectivity showed a conflict effect (iI > iC) only in the low- but not in the high-WMC group. Increases in theta power over contralateral posterior areas has been suggested to indicate involuntary shifts of attention (Ahveninen, Huang, Belliveau, Chang, & Hamalainen, 2013; Kawasaki & Yamaguchi, 2012). Applied to our findings, these group differences could reflect low-WMC individuals being captured by the task-irrelevant stimulus location, whereas high-WMC individuals may adjust more optimally to the previous-trial conflict.

Reactivity of the low-WMC participants to the previous trial conflict was further dissociated in respose-selection stage, as reflected by differences in midfrontal-to-lateral-frontal theta-band synchronization. Previously, enhanced and prolonged synchronization between MFC and lateral frontal sites has been observed in high conflict situations (cI trials and errors) and was suggested to reflect increased cognitive control demands (Cavanagh et al., 2009; Cohen & Cavanagh, 2011a; Hanslmayr et al., 2008). Here, we observed significantly stronger theta-band synchronization between MFC and lateral frontal sites on iC than iI trials in the low-WMC group, with no differences in the high-WMC group. It appears that iC trials were associated with higher response conflict in the low-WMC group. Given that spatial stimulus information in the Simon task either facilities (on congruent trials) or impedes (on incongruent trials) response selection process, it is likely that low-WMC individuals had difficulty exploiting facilitatory stimulus location on congruent trials after incongruent trials. This result again indicates that low-WMC individuals are more influenced by the task-irrelevant stimulus location than high-WMC individuals after encountering the conflict on the previous trial. This interpretation is further supported by the delta-band results, which showed that the post-incongruent conflict effect in fronto-parietal ISPC was present only for the low- and not for the high-WMC group. Although the role of delta-band activity in attention control is not well understood (Daitch et al., 2013), weaker fronto-parietal ISPC on iC trials may reflect disrupted reorienting of attention to the spatial stimulus dimension in the low- vs. high WMC group following incongruent trials.

Taken together, these findings suggest that WMC-related differences in conflict-task performance result not only from differences in conflict resolution – as suggested by Kane and Engle (2003) – but also from differences in cognitive control adjustments in response to conflict. More generally, it points to the differences in cognitive flexibility as being a key difference between high- and low-WMC participants. It appears that low-WMC individuals were less prone to use the task-irrelevant (albeit facilitatory) stimulus location on congruent trials after incongruent trials. This is similarly to previous work (Gulbinaite & Johnson, 2013; Kane et al., 2001; Unsworth et al., 2004) showing that low-WMC individuals are slower and make more errors when switching from high-conflict to low-conflict trials, particularly when switches are frequent (Gulbinaite & Johnson, 2013).

Our findings indicate that, overall, low-WMC individuals are more reactive to the contextual effects of the previous trial conflict. This is generally consistent with the idea that low-WMC individuals are more prone to resolve conflict reactively, whereas high-WMC individuals rely more on proactive cognitive control strategies (Braver et al., 2007; Burgess et al., 2011).

Conclusions. By using EEG and employing time-frequency analysis techniques, we provide novel neural evidence for the proposed relationship between individual differences in WMC and attentional control (Kane et al., 2007). The parietal theta power and fronto-parietal connectivity indicate that WMC-related differences in attention control occur early in the trial, and are modulated by the previous trial context. Later changes in theta- and delta-band fronto-parietal connectivity further highlighted group differences in flexibility to adjust top-down control in response to the previous trial conflict. These findings reveal that individual differences in cognitive control abilities are related to WMC, and that measures more sensitive than RT and error rates are required to uncover this relationship.

5 Five methodological challenges in cognitive electrophysiology

Here we discuss five methodological challenges facing the current cognitive electrophysiology literature that ad- dress the roles of brain oscillations in cognition. The challenges focus on (1) unambiguous and consistent terminology, (2) neurophysiologically meaningful interpretations of results, (3) evaluation and comparison of different spatial filters often used in M/EEG research, (4) the role of multiscale interactions in brain and cognitive function, and (5) development of biophysically plausible cognitive models. We also suggest research directions that will help address these challenges. We hope that this paper will help foster discussions and debates about important themes in the study of how the brain's rhythmic patterns of spatiotemporal electrophysiological activity support cognition.

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Introduction

Cognitive electrophysiology is a field that bridges neuroscience and psychology, and focuses on understanding how cognitive functions (including perception, memory, language, emotions, behavior control, and social cognition) are supported or implemented by the electrical activity produced by populations of neurons. The main methodological tools used by cognitive electrophysiologists are EEG and MEG, and intracranial recordings such as electrocorticogram and single- and multi-unit recordings. Although these methods span a range of species and spatial scales, they all share the common feature that they measure electromagnetic activity. Thus, the major assumption underlying the broad spectrum of cognitive electrophysiology studies is that one key neural mechanism of processing and transferring information is (or, at least, can be understood through) electrical activity.

The purpose of this paper is to highlight and discuss five major methodological challenges facing cognitive electrophysiology. Some of these challenges are related to each other; discussing them individually is done mainly for convenience. Indeed, in several cases, addressing one challenge may help address other challenges. We focus mainly on methods and data analyses involving time-frequency-based approaches, because these are the most rapidly developing methodological approaches in cognitive electrophysiology, and, as will be described below, have a large potential for understanding neurophysiological processes underlying cognitive operations.

Some readers may disagree with the importance of some of these challenges, or could name additional challenges than the five presented here. Nonetheless, we hope that this paper will help catalyze further discussions in current trends and important future directions in cognitive electrophysiology.

Challenge 1: Widespread agreement on analysis terminology

Consider the following statistical analysis terms: correlation, ANOVA, factor analysis, and receiver operating characteristic (ROC). When someone says that they performed an ANOVA, there is no ambiguity about which sets of equations were applied to the data. Furthermore, even though the term ROC provides little insight the mathematical procedure underlying that analysis, most people with a background in engineering, math, psychology, or physics will know what an ROC analysis implies and how the results can be interpreted.

Precision and widespread agreement in analysis terminology is lacking in cognitive electrophysiology. This is problematic because inconsistent, ambiguous, or confusing terminology impedes cross-study comparisons and theory development (Gardiner & Java, 1993; Tulving, 2000). To illustrate this point, consider the following electrophysiological data analysis terms: synchronization, event-related spectral perturbation, time-frequency response, and connectivity. These and other terms are ambiguous and are often lab- or software-specific. When someone says that they found an increase in alpha synchronization, you do not know whether they mean an increase in power at one electrode or an increase in phase-based connectivity between two electrodes. This confusion arises because some researchers use the term “synchronization” to indicate the squared amplitude of the frequency band-specific filtered signal at one electrode (Pfurtscheller, 1992), whereas other researchers use this same term to indicate consistency in phase angle differences between two electrodes. However, these two analyses have very different interpretations, pu-

tative neurophysiological origins, theoretical implications, and methodological concerns. Terms like spectral perturbation (Makeig, 1993) and time-frequency response are also ambiguous, because they could refer to spectral changes expressed in power, phase, connectivity, band-specific network properties, or any number of other features of time-frequency-based analyses.

Within a field of science, there should be a one-to-one mapping between terms and their meanings (also called the incontrovertibility of terms rule; Gardiner & Java, 1993). However, cognitive electrophysiology suffers from a many-to-many terminology mapping problem: the same term can have different meanings (e.g., the term "synchronization," as described in the previous paragraph); and different terms can indicate the same mathematical procedure (e.g., inter-trial phase coherence vs. phase-locking index/value can refer to the same analysis, which assesses the consistency of phase angles at one electrode-time-frequency point over trials). The many-to-many mapping of analysis terms to mathematical procedures slows scientific progress by creating confusion about how to interpret findings reported in Results sections, and how to compare results across studies that use different terms.

Another confusing and ill-defined—but often used—term is "activation." A brain region is said to be activated (or deactivated) if its activity increases (or decreases) with respect to a baseline or control condition. Although this term is widely used in univariate fMRI analyses and relatively simple analyses of action potential data such as average spike rate, this term becomes less tractable for multi-dimensional electrophysiological activity such as field potentials (Singh, 2012). For example, if a brain region exhibits an increase in inter-trial phase clustering in the theta band, a decrease in alpha-band power, no change in gamma-band power, and an increase in theta-gamma coupling, is this brain region activated or deactivated? In some cases, increases in power that seem to lack a clear frequency structure are referred to as "activation" (Burke et al., 2013; Miller, Zanos, Fetz, den Nijs, & Ojemann, 2009), but this approach may obscure the fine temporal structure of activity, such as multiple overlapping frequencies (Crone, Korzeniewska, & Franaszczuk, 2011) or temporal or correlation-based information coding (Engel, König, Kreiter, Schillen, & Singer, 1992).

Perhaps the lack of terminological convergence was less of a concern a few decades ago, when few research groups were performing time-frequency-based analyses, and most analyses were based on the squared amplitude of the frequency band-specific signal (i.e., power). However, the lack of consistency in analysis terminology becomes problematic as more scientists begin applying sophisticated data analyses. With varied and sometimes ambiguous terminology, rapid and efficient cross-study comparisons become increasingly difficult.

The challenge, therefore, is to adopt a widely accepted and unambiguous terminology for describing multivariate changes in electrophysiological data. We recommend using analysis terms that closely and succinctly reflect the mathematical procedure applied to the data (Cohen, 2014), rather than using terms that reflect interpretations of putative neurophysiological events underlying time-frequency features. For example, when extracting the energy of a frequency band-specific signal (the squared amplitude), the term "power" should be preferred over terms such as "synchronization" because "power" is an unambiguous description of the analysis, whereas synchronization is a speculative interpretation of a result (in this case, that the neural networks measured by the electrode became synchronized;

Pfurtscheller & Lopes da Silva, 1999). At least in the context of electrophysiology data, it might be best simply to avoid using functional univariate terms like "de/activation." Instead, terms could describe the statistical properties of the data, such as "relatively increased power in the beta-band," or "correlation between alpha phase and gamma power." In Table 5.1, we suggest analysis terms for some commonly used analyses.

Table 5.1. Suggested terminology for time-frequency-based M/EEG data analyses. See Cohen, 2014, for more in-depth discussions and justifications of each term.

Preferred term	Description	Examples of less preferred terms
Power	Squared amplitude of frequency-band specific time series	Synchronization/desynchronization, ERS/ERD, ERSP, TFR
Inter-trial-phase-clustering	Length of average vector from a distribution of unit phase angles at one time-frequency point over trials.	Phase-locking, phase-coherence, phase-reset
Inter-site-phase-clustering	Length of average vector from a distribution of unit phase angle differences between two electrodes at one time-frequency point over trials.	Phase-locking, phase coherence, coherence, synchronization, coupling, phase correlation

Notes. Terms are less preferred if they are ambiguous, imprecise, or are interpretations of putative neural events rather than descriptions of analysis methods. ERS=event-related synchronization; ERD=event-related desynchornization; ERSP=event-related spectral perturbation; TFR=time-frequency response.

Challenge 2: Neurophysiological interpretation of time-frequency results

The mathematical development of time-frequency-based data analyses, and their applications to studying cognition, have advanced beyond the understanding of the neurophysiological events that might underlie the results of those analyses. For example, the difference between phase-locked and non-phase-locked (also known as evoked and induced, respectively) activity remains unclear, with theory and models suggesting complex interactions between neurobiological events that may be measured as phase-locked vs. non-phase-locked events (Burgess, 2012; David, Kilner, & Friston, 2006; McLelland & Paulsen, 2009; Tallon-Baudry & Bertrand, 1999), but little empirical data to provide firm conclusions. Another example is functional connectivity estimated between two electrodes, which can be based on correlations in frequency band-specific power time series (Bruns, Eckhorn, Jokeit, & Ebner, 2000), or on a clustering of phase value differences (Lachaux, Rodriguez, Martinerie, & Varela, 1999). It is unclear whether connectivity based on power and on phase reflect similar mechanisms (e.g., long-range activation of inhibitory interneurons; Bush & Sejnowski, 1996), and it is unknown whether the same mechanisms underlie connectivity in different frequency bands or in different brain regions.

The challenge, therefore, is to gain a better understanding of the neurophysiological events that lead to time-frequency phenomena observed at the scalp, including power, phase, and various measures of connectivity. Of course, much is known about the biophysical properties of neurons and volume conduction through head tissues that allow the M/EEG to be measured (Lopes da Silva & van Rotterdam, 1982). However, much less is known about the kinds of cellular, synaptic, neurochemical, and systems-level processes that produce the complex multi-frequency dynamics that have been linked to cognition. Meeting this challenge will move cognitive electrophysiology forward: At present, EEG data are typically treated and discussed in terms of abstract "time-varying brain signals." Although this is an accurate description, the patterns observed in EEG data are not arbitrary signals, but rather, are direct measurements of complex biophysical processes from which cognition, emotion, language, and myriad other functions emerge. As patterns in EEG data can be better linked to both micro- and mesoscopic-level neural processes, the understanding of neural machinery and computations underlying cognitive processes will improve.

This challenge has already received some empirical and theoretical attention (Wang, 2010). For example, gamma oscillations are known to be driven by interactions between excitatory and inhibitory cells (Buzsaki & Wang, 2012). Other features of EEG data have less clear origins. For example, response conflict elicits increased activity in the theta-band (4-8 Hz) over midfrontal regions (Cavanagh et al., 2009; Cohen, 2011c; van Steenbergen, Band, & Hommel, 2012). *Why* does response conflict elicit midfrontal theta, and not alpha, or beta, or gamma? What does this indicate about the neural computations that identify and resolve conflict? At present, there are few clear answers to this and many other questions about why specific cognitive processes are associated with specific patterns of spectral responses (Donner & Siegel, 2011).

Not all relevant EEG dynamics are localized to specific frequency bands. Indeed, some task-related electrophysiological features seem to lack frequency band specificity, instead comprising broadband changes in power (Burke et al., 2013; Crone et al., 2011; He, Zempel, Snyder, & Raichle, 2010; Manning, Jacobs, Fried, & Kahana, 2009; Miller et al., 2009). This broadband activity may reflect increases in asynchronous multi-unit activity, or frequency band-specific but transient patterns (Crone et al., 2011; Rieke, 1999). Indeed, broadband gamma activity (60-200 Hz) seems to correlate more strongly with inter-neuronal synchrony than with average firing rate (Ray, Crone, Niebur, Franaszczuk, & Hsiao, 2008).

Of the five challenges discussed here, this one is the most difficult for cognitive electrophysiologists who study humans to address. This is because understanding the neurophysiological bases of non-invasive scalp M/EEG signals requires methodological approaches that are outside the typical cognitive electrophysiology lab and expertise, such as simultaneous invasive and non-invasive recordings. Some of this type of research has already been done, for example by studying the relationship between individual neurons and field potentials (Coenen, 1995; Kraut, Arezzo, & Vaughan, 1985; Schroeder, Tenke, Givre, Arezzo, & Vaughan, 1991; Whittingstall & Logothetis, 2009). Other studies have provided evidence that local field potentials are driven mainly by synchronous spiking or bursting of cell assemblies, whereas individual spikes (which may reflect neural noise) contribute significantly less to the local field potential (Denker et al., 2011; Kelly, Smith, Kass, & Lee, 2010; Silva, Amitai, & Connors, 1991). But oscillations are more than simply the sum of presynaptic spikes: Many intra- and inter-neuronal signals contribute to oscillations (Buzsáki et al., 2012), including dynamic intra-laminar and cortical-thalamic interactions (Hindriks & van Putten, 2013; Jones et al., 2009). Due to intrinsic membrane properties, individual neurons can be "tuned" to specific frequency bands, such that their firing probability depends both on the phase and the frequency of the local field potential, a phenomenon known as spike-field coherence (Fries, Schröder, Roelfsema, Singer, & Engel, 2002). One major limitation common to these studies is that they typically do not record EEG as it is used in humans (5-10 mm diameter ring electrodes placed outside the head); thus it is not clear to what extent the relationship between neurophysiological events such as spiking are related to the EEG signal recorded in humans.

A better understanding of the neurophysiological processes that underlie the time-frequency features observed in scalp-recorded M/EEG would require a two-step approach. The first step would involve simultaneous microscopic and macroscopic recordings to characterize the activity at the level of individual neurons and populations of neurons during different scalp-recorded EEG events that have been linked to cognitive processes. Such research should be done in different brain regions using a variety of cognitive tasks, because the mechanisms underlying, for example, visual cortex alpha and prefrontal cortex alpha may be different. Most importantly, for the findings to be relevant to human cognitive electrophysiology, the research would have to use electrodes that are used in humans. The second step would involve causal interventions to test specific hypotheses about the relationship between neurophysiological phenomena and scalp-recorded EEG signals. Optogenetics may be a promising approach (Fenno, Yizhar, & Deisseroth, 2011; LaLumiere, 2011), because specific types of neurons can be activated using time courses specified by the researcher. For example, it was shown that activating fast-spiking inhibitory interneurons can increase gamma-band oscillations in local field potentials, which in turn facilitate sensory perception (Cardin et al., 2009) and suppress lower frequency oscillation power (Sohal, Zhang, Yizhar, & Deisseroth, 2009). Whether and how these local changes would be measurable at the level of scalp EEG remain to be determined.

Challenge 3: Reconciling the many diverse spatial filters used in cognitive electrophysiology

Spatial filters use weighted combinations of electrode (or sensor) activity to isolate features of the data that may be difficult to observe in the spatially unfiltered data. The spatial filters that are commonly used in cognitive electrophysiology include independent components analysis, principle components analysis, the surface Laplacian (also sometimes called current source density, current scalp density, or dural imaging), single dipole fitting, static distributed source imaging such as LORETA, and adaptive distributed source imaging such as beamforming. Of course, it is also very common not to apply any spatial filters, and instead to analyze the spatially unfiltered electrode- or sensor-level data.

Spatial filters were not widely used in the history of cognitive electrophysiology. However, as the algorithmic development of spatial filters improves, and as M/EEG recording technology (e.g., more than 100 electrodes) allows higher quality recordings with more electrodes, spatial filters will become increasingly important and commonly used. There are three main advantages of using spatial filters (Cohen, 2014): they allow improved localization of activity to topographical or brain regions, they facilitate the appropriateness and interpretation of connectivity analyses, and they can reveal features of the data that are not readily visible in the spatially unfiltered data (analogously, gamma-band oscillations can be difficult to observe in EEG data without temporal filtering).

The issues we raise here are that different spatial filters can be qualitatively different from each other, highlight different features of the data, and have very different sets of parameters and assumptions. An example can be seen in Figure 5.1, which shows data from one subject (taken from Cohen & Ridderinkhof, 2013) that were analyzed using three different spatial filters (surface Laplacian, independent components analysis, and beamforming) and no spatial filter. Both commonalities and divergences can be seen in the results.

There is no clear consensus regarding which spatial filters should be used in which situations, which analysis and brain-functional assumptions are made by different kinds of spatial filters, which parameter settings are appropriate for which kinds of data, and, importantly, which kinds of interpretations are valid and appropriate for each spatial filter. The qualitative differences among spatial filters, and the lack of clear understanding and consensus concerning the various spatial filters, hinders comparisons and meta-analyses, and causes confusion or misinterpretations amongst scientists who are not experts in using or interpreting results from spatially filtered data. Indeed, many discussions about this issue seem to occur more often in informal discussions than in the scientific literature, making it difficult for non-experts to know which spatial filters to use or how to evaluate results of different spatial filters.

The challenge, therefore, is to build a consensus for the situations in which each spatial filter is appropriate (including, for example, the kind of data and expected distribution of neural generators), and the kinds of interpretations that are appropriate to make from different spatial filters. Reviewing the assumptions and practical implementations of all spatial filters is a task too great and too lengthy for this review. Here, as an example of the differences in spatial filters, we highlight two specific filters that are used in connectivity analyses: Beamforming and the surface Laplacian. Beamforming is an adaptive spatial filter that utilizes the covariance between a forward model (an estimate of the scalp-measured signal given activity in a location in the brain) and the observed electrode-level data to estimate the potential brain sources of scalp-observed signals. Beamforming relies on several assumptions about brain and head shape, the strength of correlated sources, the orientations of dipoles, and, for EEG, the conductances of different head tissues. The surface Laplacian is a spatial band-pass filter that attenuates spatial low-frequency components, which often reflect volume-conduced sources. The surface Laplacian relies on few assumptions and parameters (except spatial smoothness), but is limited to scalp-level inferences. Despite their differences, both spatial filters have been recommended for inter-regional connectivity analyses (Schoffelen & Gross, 2009; Srinivasan et al., 2007), but, to our knowledge, these have not been directly compared. It is unclear from the literature which of these two spatial filters is best for connectivity analyses in which circumstances.

This challenge can be addressed in two ways. First, there can be dedicated methods papers that compare results of different spatial filters using simulated data as well as real data that likely have distributed brain generators (an online dataset has recently been made available specifically for this purpose; Aine et al., 2012). Although simulated data are useful because the ground truth is known, they often lack realistic characteristics of EEG data, including noise, traveling waves, and brain region interactions, and may be biased towards specific methods. Real datasets, on the other hand, are likely to provide more insights into practicalities of spatial filters, but it may be difficult to know what the “true” result is when different spatial filters produce different results. Much of the extant literature comparing

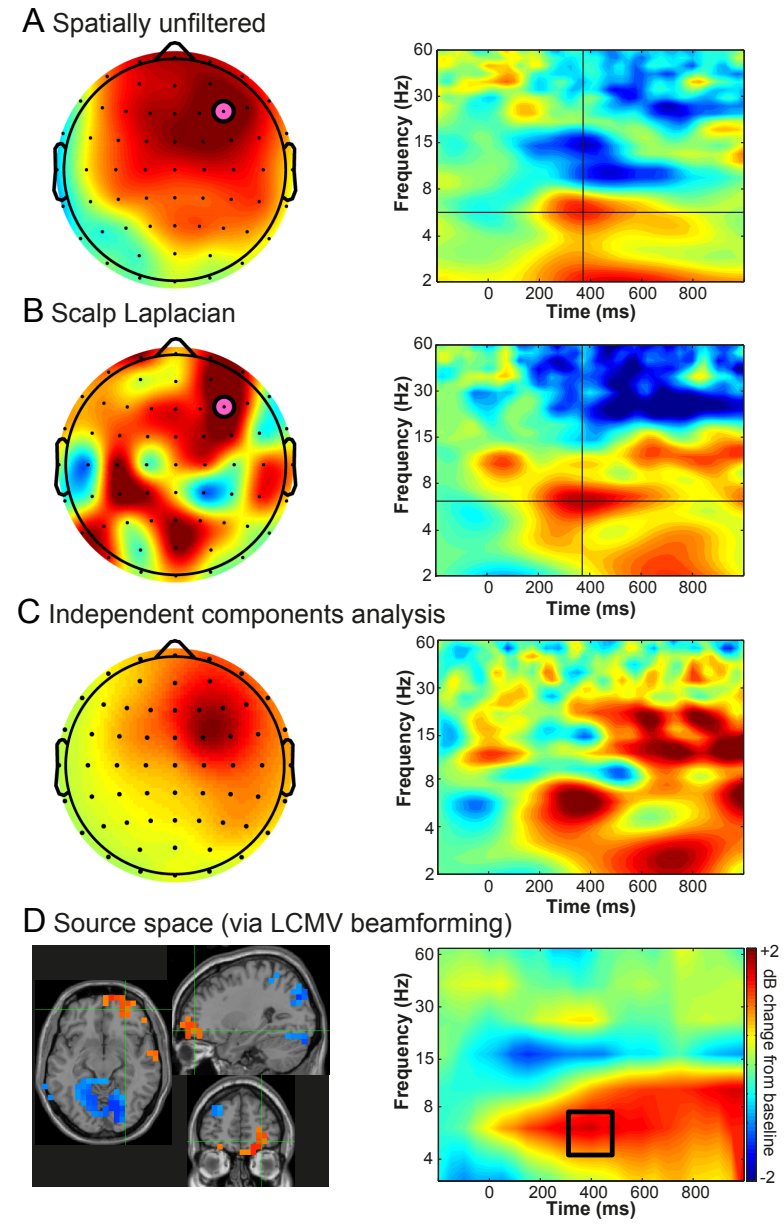

Figure 5.1. Illustration of results of different spatial filters applied to the same single-subject dataset. The right-hand panel shows a time–frequency power plot from electrode FC4 for panels A and B (see pink electrode), an independent component that was selected based on its topographical distribution (panel C), and a single voxel from a distributed source imaging analysis (LCMV beamforming; see green crosshairs in panel D). Although there are clearly some similarities, for example, in the ~200–500 ms increase in theta-band power, there are also differ- ences in topography and time–frequency features, such as the ~15–50 Hz relative power suppressions.

spatial filters focuses on comparing parameter settings for the same filter, or comparing different algorithms for the same type of filter (Dalal et al., 2008; Hansen, Kringelbach, & Salmelin, 2010; Hauk, 2004; Michel et al., 2004). These investigations are extremely useful for within-filter comparisons; future studies should additionally focus on comparisons across spatial filters.

The second way to address this challenge is in studies that are content-oriented (as opposed to being specifically methods-oriented). Here, analyses can be performed with a few different spatial filters to determine whether and how the results depended on the specific spatial filter. It is likely that qualitative differences among spatial filters will arise in more detailed analyses, such as inter-regional frequency band-specific connectivity, or when considering complex frequency patterns (Figure 5.1). Two examples from the literature highlight that in different situations, spatial filters can have little (Cohen, 2011a) or significant (Rivet, Cecotti, Maby, & Mattout, 2012) effects on the results.

Of course, the spatial accuracy of EEG and MEG is limited compared to fMRI or invasive recordings. Nonetheless, there is considerably more spatial information available in high-density recordings (>100 electrodes) than in the low-density recordings (<33 electrodes). As the spatial information available in the M/EEG data continues to increase, and as an understanding of distributed network functioning becomes increasingly relevant in cognitive electrophysiology, building a consensus about spatial filters becomes an important challenge to be met.

Challenge 4: Characterizing multi-scale interactions in neuroelectric activity

Spatial and temporal multiscale interactions are thought to be a defining feature of the brain (Figure 5.2), and a critical principle that underlies cognitive functions and consciousness (Breakspear & Stam, 2005; Le Van Quyen, 2011; Varela, Lachaux, Rodriguez, & Martinerie, 2001). The cognitive electrophysiology literature spans a broad range of spatiotemporal scales: Spatial scales range from single unit firings (a very small spatial scale) to local field potentials (a relatively small spatial scale) to source-reconstructed EEG or MEG activity (a relatively medium spatial scale) to low-spatial-resolution EEG (i.e., fewer than 33 electrodes; a relatively large spatial scale); temporal scales range from milliseconds (e.g., spike timing) to minutes (e.g., resting-state). In some cases, spatial and temporal scales may be related. For example, in the motor system, beta-band activity appears to be relatively spatially widespread while gamma-band activity appears to be more spatially restricted (Miller et al., 2007). However, time and space are not necessary linked, and the idea that, for example, lower temporal frequencies correspond to larger brain networks (von Stein & Sarnthein, 2000) is a useful conceptualization but is not fully consistent with empirical findings. For example, large-scale brain networks can also be entrained in the gamma band (Doesburg, Roggeveen, Kitajo, & Ward, 2008; Pesaran, Nelson, & Andersen, 2008; Siegel, Donner, Oostenveld, Fries, & Engel, 2008).

Despite the theoretical importance of multiscale interactions for brain function, most individual cognitive electrophysiology studies utilize only one spatial and temporal scale. This means that comparisons across spatial and temporal scales are often made loosely and qualitatively, across different studies. The challenge, therefore, is to determine to what extent dynamics at different spatial and temporal scales are related to each other, and to determine how these multiscale dynamics are in turn related to cognitive processes.

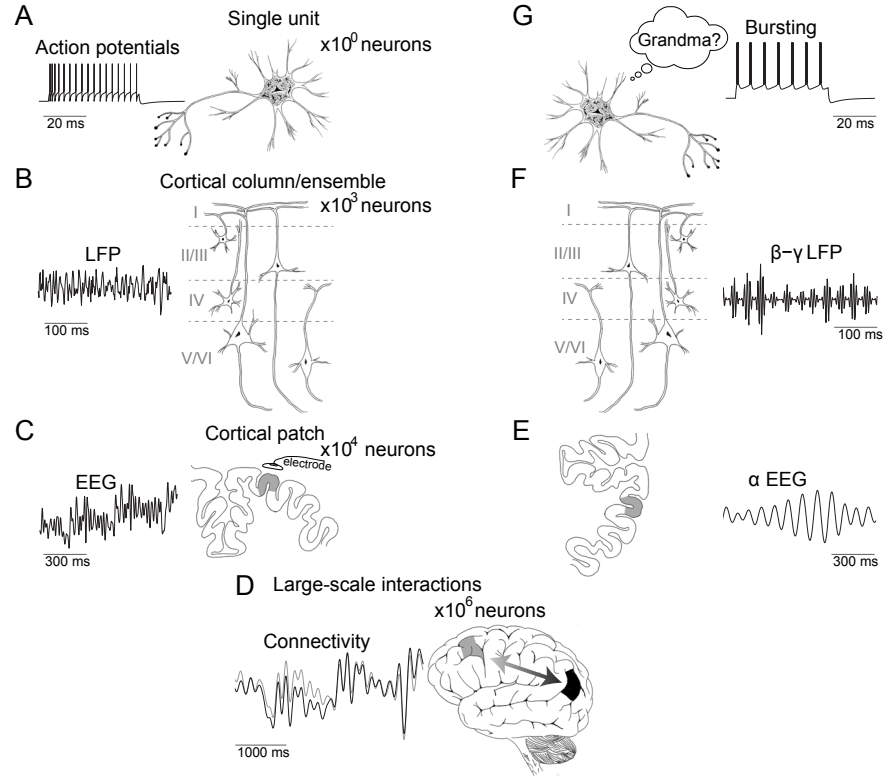

Figure 5.2. To understand the information content of neural dynamics at one spatiotemporal scale, it might be necessary to consider the neural dynamics at other spatiotemporal scales. (A) A single neuron emits action potentials in response to a stimulus. The information contained in action potential timing may depend on the simultaneous activity of the neural ensemble in which that neuron is embedded (B). The collective activity of the ensemble can be measured as the local field potential (LFP), which can encode information in different frequencies simultaneously, and can also functionally connect neighboring neural ensembles. (C) These synchronous neural ensembles form cortical "patches" that produce electrical fields large enough to be recorded with the EEG. (D) Large-scale brain networks become synchronized, for example, during top-down control processes such as attention. The processes depicted in panels A-D are often termed "bottom-up," because the spatiotemporal scales are increasing. These same pathways are also used for "top-down" processes, as illustrated in panels D-G. Top-down processes such as attention can modulate neural activity at cortical patches, (F) which in turn can regulate activity in neural ensembles, (G) which in turn can modulate activity of single neurons. Sub-neuron-level dynamics (e.g., synapses) and supra-brain dynamics (e.g., inputs from other body systems such as digestion, breathing, and heart rate) are not depicted here, but are also relevant for brain function and neural computation.

A better understanding of multiscale interactions is important for two reasons. First, the mechanisms that govern brain function at one spatiotemporal scale and in one brain region may not generalize to other spatiotemporal scales and other brain regions. Second, mechanisms that are observed at one spatiotemporal scale may be difficult or impossible to explain without understanding mechanisms at larger or smaller spatiotemporal scales. An

example of this latter phenomenon is that the timing of an individual action potential may seem random until discovering that that action potential is locked to a specific phase of the local field potential.

There are several possible approaches to address this challenge. Most importantly, addressing this challenge will require a widening of perspectives on the role of multiscale interactions in brain function. Most scientists would agree that multiscale interactions are important for brain function, and yet few incorporate these ideas into empirical research. For example, in EEG research it is typical to filter out activity at both low (<1 Hz) and high (>40 Hz) frequencies; thus, potentially relevant multiscale temporal interactions are not considered (Palva & Palva, 2012).

Second, theories will need to be developed in order to make predictions, guide analyses, and interpret results concerning multiscale interactions (see also challenge 5 concerning the role of theories in cognitive electrophysiology). An illustration of a theory that makes testable predictions for multiscale temporal interactions comes from working memory studies (Axmacher et al., 2010; Jensen & Lisman, 1998; Sauseng et al., 2009), in which the number of gamma cycles observed in a theta cycle (e.g., cross-frequency coupling; a temporal multiscale phenomenon) is thought to vary as a function of memory load or memory capacity. What specific predictions about multiscale interactions could be made regarding other cognitive processes such as action monitoring, learning, decision-making, language, and social imitation?

Third, this challenge will require developments in data acquisition techniques. Most brain imaging technologies are designed to measure one spatial scale; studying spatial multiscale relationships often requires specialized equipment that may be difficult to access or that may require considerable technical expertise (for example, simultaneous single-cell electrophysiology and fMRI). Multiscale interactions can also be measured by combining methodological approaches at different spatial scales, such as combined EEG-FMRI (Debener et al., 2005; Jann et al., 2012). In this case, the FMRI signal has higher spatial resolution while EEG has higher temporal precision.

Relatedly, there will need to be developments in the data analyses that are used to quantify and conceptualize multiscale interactions. At present, multiscale temporal interactions are most often assessed through cross-frequency coupling (Lisman & Jensen, 2013). Cross-frequency coupling has been related to information processing schemes (Lisman, 2005), and there are many empirical demonstrations of cross-frequency coupling characteristics being modulated by cognitive task demands (Canolty & Knight, 2010; Cohen & van Gaal, 2012; Kayser, Ince, & Panzeri, 2012; Voytek et al., 2010; Young & Eggermont, 2009). Graph theory provides some useful metrics for characterizing how local activity can be modulated by network-level dynamics (e.g., Eldawlatly, Jin, & Oweiss, 2009). In some cases, both temporal and spatial multiscale interactions can be examined simultaneously (Le Van Quyen, Botella-Soler, & Valderrama, 2013; van der Meij, Kahana, & Maris, 2012).

Challenge 5: Developing neurophysiologically grounded psychological theories

Theories facilitate scientific development. They provide frameworks for generating new experiments and hypotheses, interpreting results, and comparing results across methodologies, species, and levels of analysis (Abbott, 2008). Theories that provide an interface

between psychological constructs and neural dynamics are particularly important, because the gap between, for example, the action potentials of a neuron in visual cortex and the subjective report of having seen a briefly flashed visual stimulus, is quite large; good theories can help bridge these kinds of distances.

The challenge is to develop and expand theories that can account for and make specific predictions regarding cognitive processes *and* the neurophysiological dynamics that accompany those processes (including frequency band-specific responses, connectivity, etc.). At present, many psychological theories that make predictions for brain activity assume that cognitive functions are localized to specific brain regions, and that the operation of a cognitive function can be measured as "activation" of that brain region (see challenge 1 for a discussion of the term activation). These types of "cognitive-level" models have been important for the development of cognitive science and cognitive neuroscience, and we do not intend to criticize this approach generally. However, it has become clear that at the electrophysiological level, predictions of cognitive models that assume a unidimensional "activation/deactivation" scale for brain activity become neither confirmable nor falsifiable.

The under-specification of neurophysiological dynamics in psychological theories presents both theoretical and statistical concerns. Theoretically, predictions concerning neurophysiological implementations become difficult to confirm or disprove, in part because the search space in which a feature of data can be post-hoc labeled "activation" is large. For example, imagine a theory that predicts increased activation in a brain region, and two experiments are carried out to test this prediction. One experiment finds an increase in theta-band power, decrease in alpha-band power, and increased inter-regional connectivity; the other experiment finds no change in theta- or alpha-band power, increases in beta- and gamma-band power, and increases in theta-gamma coupling. The results of these two experiments are quite different; which experiment is more consistent with the theory? In this case, the answer is neither, because the theory is too under-specified to help resolve the inter-experiment inconsistencies.

This theoretical concern is further compounded by a statistical concern: The high-dimensional space of electrophysiology time-frequency results provides a large number of statistical evaluations, which require appropriately strict statistical correction for multiple comparisons. Without better theories that make more precise predictions, statistical sensitivity may be too low to detect subtle but true findings when correcting for multiple comparisons over time, frequency, and space (Ashton, 2013). Furthermore, without theoretical guidance, the researcher might fail to recognize a true finding when it is present in the data.

Addressing this challenge will require a deeper integration between cognitive psychology, electrophysiology, and biophysical principles. Fortunately, making this connection becomes easier, with developments in neuroscience, computing, and electrophysiology. For example, there are now simplified computational models that contain sufficient biophysical plausibility to simulate local field potential and EEG data, such as neural mass and neural field models (Babajani-Feremi & Soltanian-Zadeh, 2010; Deco, Jirsa, Robinson, Breakspear, & Friston, 2008; Nguyen Trong, Bojak, & Knösche, 2012). Furthermore, specialized software for simulating small- and large-scale networks of biophysically plausible neurons are under constant development (e.g., "NEST": Gewaltig & Diesmann, 2007; "Brian": Goodman & Brette, 2008; "NEURON": Hines & Carnevale, 1997). Although many biophysical models do not exhibit cognitive behaviors and many "cognitive-level" theories do not contain

biophysical plausibility, there are no longer major scientific or practical stymies that prevent deeper links between cognitive and electrophysiology. The development of theories that account for both neurophysiological and psychological phenomena may prove to be transformative for the field of cognitive electrophysiology.

There are several theories that bridge cognitive processes and physiological mechanisms, and therefore meet this challenge. Following are three examples. First, one recent theory (Jensen, Bonnefond, & VanRullen, 2012) incorporates both the putative biophysical mechanisms of alpha oscillations and the cognitive consequences in terms of when salient or attended visual stimuli can be processed. Second, there are theories of working memory that explain how reverberatory activity in biophysically plausible neural networks can be used to maintain goal-relevant representations that are robust against distracters (Amit & Brunel, 1997; Compte, Brunel, Goldman-Rakic, & Wang, 2000). Third, theories of simple perceptual decision-making provide putative biophysical circuit mechanisms underlying simple sensory discrimination (Wang, 2012). These are not the only examples; other models contain some biophysical plausibility and can also explain some aspects of sensory, perceptual, and cognitive phenomena (Ardid, Wang, Gomez-Cabrero, & Compte, 2010; Buia & Tiesinga, 2006; Corchs & Deco, 2002; Wiecki & Frank, 2013). Nonetheless, many cognitive processes and their neurophysiological correlates are not accounted for by current theories. Indeed, the claim that "electroencephalography is still mainly an empirical science" (Zhadin, 1984) is as true now as it was 30 years ago.

New horizons in cognitive electrophysiology

This is an exciting time to be a cognitive electrophysiologist. Developments in M/EEG recording equipment provide increasingly higher quality data, and developments in computing technology allow increasingly sophisticated analyses of those data. Furthermore, developments in neuroscience, neurobiology, and biophysical modeling allow researchers to link their scalp-recorded findings (in particular, findings suggesting large-scale oscillatory dynamics) to neurophysiological mechanisms with a level of detail not previously possible in the history of non-invasive EEG. The next few decades are likely to see significant and possibly qualitative improvements in understanding how cognitive functions are produced by multiscale integrative electrophysiological dynamics. These developments will likely outpace the developments over the previous decades, considering for example that the link between inter-regional spectral coherence and learning was already known in the 1970's (Busk and Galbraith, 1975).

To be sure, there is much yet to learn. Perhaps in the year 2033 we'll look back and marvel at how primitive and uninformed our theories and analyses were in the year 2013. Our aim in this paper was to point out some of the methodological challenges that, if met, will help cognitive electrophysiology develop as a science into the 21st century.

6 General Discussion

"...the teacher gave the following instruction to Jay: *"Put your sheets on the green table, put your arrow cards in the packet, put your pencil away and come and sit on the carpet ."*" (Gathercole & Alloway, 2008) Jay was not able to follow all of teacher's instructions because he simply forgot some of them. Evidence suggests that WM capacity predicts our ability to acquire knowledge and develop new skills (Pickering, 2006), and is a better predictor of academic achievement than IQ (Alloway & Alloway, 2010). Variations in WMC are related to language learning (Linck et al., 2013; Szmalec et al., 2012), reading comprehension (Daneman & Carpenter, 1980; Pimperton & Nation, 2012), and novel problem solving (Engle, Tuholski et al., 1999; Kane et al., 2004). However, the underlying neurobiological mechanisms that drive variations in WMC are not well understood (Burgess et al., 2011). Identifying the neural mechanisms of WMC differences has broad implications. On the theoretical level, it may lead to neurophysiologically plausible theories that allow testing more specific predictions (Chapter 5). On the practical level, it may provide better targets for training programs, and more accurate evaluation of training effects (Buschkuehl et al., 2012; Langer, von Bastian, Wirz, Oberauer, & Jancke, 2013).

Understanding the neural basis of broad constructs such as WMC has been proven to benefit from investigation of related processes that can be directly measured (Miyake & Friedman, 2012). In this thesis, we exploited the often-observed relationship between WMC and performance in response-conflict tasks (e.g., Simon task, Eriksen flanker), which challenge one's ability to maintain task goals in the face of distraction from habitual response tendencies. By characterizing the relationship between WMC and cognitive control abilities combining different analyses and experimental approaches we sought to extend WMC research from cognitive to the neural level.

"You can go with this or you can go with that"[1]

The behavioral study described in Chapter 2 of this thesis was designed to test the hypothesis that high- as compared to low-WMC individuals not only are better at keeping task instructions in mind, but also are faster at resolving interference between task-relevant and task-irrelevant information – as suggested by executive-attention theory of WMC (Kane et al., 2007; Kane & Engle, 2003). We used the Simon task, in which the task-relevant stimulus feature (shape) and the task-irrelevant feature (location) can be congruent (no response conflict) or incongruent (elicits response conflict). The ratio of congruent and incongruent trials was kept the same to facilitate maintenance of the task goal and to isolate possible WMC-related differences in conflict processing. The difficulty of conflict resolution was manipulated by changing proportion of congruency repetitions (congruent trials followed by congruent, and incongruent trials followed by incongruent) and congruency alternations. Given that congruency alternations are associated with stronger response-selection conflict (Hommel et al., 2004), and that the higher proportion of congruency switches increases unpredictability of the task environment[2], we hypothesized that WMC-related differences

[1] Fat Boy Slim (2000). *Weapon of Choice.*

[2] From an information theory perspective, in a completely balanced four-stimuli sequence participants would be placed under 2.00 bits of response uncertainty (Mordkoff, 2012). Average uncertainty in our dataset was 1.94, 1.96, and 1.97 for 75%-, 50%-, and 25%-repetition condition. That is, predictability decreased as the number of congruency alternations increased.

should be especially evident when congruency alternations are predominant, which imposes the highest demands on cognitive control.

Mean RT analyses supported our contention, as RTs monotonically decreased when proportion of congruency alternations decreased and was stable across conditions when proportion of congruency alternations increased, suggesting an additive effect of task practice and increase in difficulty. Sensitivity to the task context varied as a function of WMC: the low-WMC group (1st quartile of the distribution) but not the high-WMC group (4th quartile of the distribution) showed a decrease in the Simon effect as the task became more difficult. Examination of the entire RT distribution using delta-plots (interference effect for RTs plotted as a function of response time) revealed that WMC-related differences in conflict processing were apparent only in the most difficult condition, such that low-WMC scores were associated with steeper negative-going delta plot slopes. Taking into account that the steepness of the slope has been interpreted as the strength of reactive control (Forstmann, Jahfari et al., 2008; Forstmann, van den Wildenberg et al., 2008; Winkel et al., 2011; Wylie et al., 2010), this finding suggests that low-WMC individuals tend to rely on reactive conflict resolution even in the condition that "rewards" a more proactive approach because the need for control is high.

In conclusion, these findings support Kane and Engle's (2003) idea that WMC-related differences in interference effects not only are related to variability in goal-maintenance abilities, but also reflect variations in conflict processing. Importantly, these results could not have been derived had we relied on mean RT analyses only. Moreover, these findings also indicate that individual differences in the speed of conflict resolution are context dependent. Although high-WMC individuals are able to engage in a proactive control strategy and thus resolve conflicts faster, the ability is related to the utility of such strategy in context-dependent manner.

"You start to walk towards the station. I walk towards the bus"[3]

Individuals scoring high on WMC measures are less susceptible to visual and auditory distractions (Conway et al., 2001; Kane & Engle, 2003; Unsworth et al., 2004; Vogel & Machizawa, 2004), indicating more efficient filtering of irrelevant information (Cowan & Morey, 2006; Vogel et al., 2005). However, whether WMC-related differences in selective attention reflect differences in suppression of irrelevant information, or enhancement of relevant information, or a combination of both remains an open question. In Chapter 3, we directly addressed this question by "frequency tagging" the relevant and irrelevant information in the Eriksen flanker task. "Frequency tagging" method is based on the observation that repetitive visual stimulation elicits a series of evoked responses (steady state visual evoked potentials; SSVEP), which have distinct frequency characteristics in EEG that match stimulation frequency and thus can be used to quantify the amount of attention paid to several simultaneously presented stimuli (Muller, Teder-Salejarvi, & Hillyard, 1998; Regan, 1977).

We found that WMC is related to the control of attention to both relevant *and* irrelevant information (Sauseng et al., 2009). Already during preparation for the imperative stimulus when participants were presented with the placeholder array (with the same number of stimuli as the imperative stimulus) WMC-related differences in distribution of attention

[3] Brian Eno and John Cale (1990). *Cordoba.*

between target and distractors were evident. While high-WMC individuals expressed stronger relative suppression of the distractors, low-WMC individuals expressed stronger relative enhancement of the targets. Given that behavioral performance was similar between the two groups, the finding suggests that high- and low-WMC individuals use different strategies to perform the task.

These findings have two important implications. First, it offers a possible explanation for why the relationship between selective attention and WMC is not always found in some tasks that are specifically designed to challenge attention control abilities (Heitz & Engle, 2007; Keye et al., 2013; Morey et al., 2012; Wilhelm et al., 2013). That is, a deficit in suppression of irrelevant information can be counterbalanced by an attentional facilitation of processing of relevant information. Second, individual differences in ability to suppress irrelevant information might have a stronger impact on WMC measures (e.g. operation and symmetry span tasks), whereas for other attention-demanding tasks relative differences between enhancement of relevant and suppression of irrelevant information are more likely to be important.

"Intergalactic planetary. Another dimension, another dimension"[4]

Executive-attention theory proposes a close relationship between WMC and cognitive control abilities. However, weak effects or null findings are often reported between WMC measures and behavioral measures of cognitive control (interference effect and congruency sequence effects; Table 1 in the Introduction section of Chapter 1). We hypothesized that measuring neural dynamics of conflict processing and adaptation to conflict could be a more sensitive approach to detect WMC-related individual differences. Therefore, in the study presented in the Chapter 4, we tested this hypothesis by measuring EEG during the Simon task and applying time-frequency analysis techniques. WMC-related differences in response-conflict tasks are mostly evident on post-incongruent trials (Gulbinaite & Johnson, 2013; Hutchison, 2011; Keye et al., 2009; Weldon et al., 2013). To constrain multidimensional condition-time-frequency-region search space we focused on post-incongruent trials only and investigated changes in theta (4-8 Hz) oscillatory activity in fronto-parietal network, which has been associated with cognitive control processes (Cohen & Ridderinkhof, 2013).

Behaviorally, group differences in the conflict effect following incongruent trials showed a pattern in the predicted direction (larger reverse Simon effect for low- compared to high-WMC group) but were not statistically significant. Similarly, replicating the findings of the Eriksen flanker task (Chapter 3), localized activity as measured by oscillatory theta-band power over midfrontal areas did not show significant group differences. Phase synchrony in fronto-parietal network, on the other hand, revealed group differences in conflict adaption already early in the trial. Low-WMC individuals were more reactive to the to-be-ignored stimulus location, whereas high-WMC individuals adjusted to the previous trial conflict more optimally. Synchrony patterns between midfrontal and lateral-frontal areas in theta band, and between midfrontal and anterior parietal sites in delta band further highlighted group differences in reactivity to the previous trial conflict. Low-WMC individuals had difficulty exploiting facilitatory stimulus location on congruent trials after incongruent

[4] Beastie Boys (1998). *Intergalactic.*

trials, indicating again that low- compared to high-WMC participants over-reacted to the previous trial conflict. These findings are consistent with the conclusions drawn in Chapter 2, that low-WMC individuals are more prone to resolve conflict reactively, whereas high-WMC individuals rely more on proactive cognitive control strategies (Braver, 2012; Braver et al., 2007).

Using EEG signatures of performance monitoring, such as synchronous local and inter-areal changes in oscillatory activity in theta/delta frequency bands, we showed that high- and low-WMC individuals differ in trial-to-trial adjustments in cognitive control. These findings extend the executive-attention theory of WMC (Engle & Kane, 2004; Kane et al., 2007; Kane & Engle, 2003), and elaborate on the possible neural mechanisms underlying WMC-related differences in cognitive control. It appears that the relationship between WMC and cognitive control abilities is more strongly reflected in large-scale oscillatory network dynamics than in spatially localized activity or in behavioral task performance.

Conclusions and Future directions

The research described in this thesis was motivated by one of the cognitive theories of WM – the executive-attention theory of WMC (Engle & Kane, 2004; Kane et al., 2007; Kane & Engle, 2003). The theory suggests a close relationship between individual's WMC and attention control abilities in the face of interference from habitual action routines, environmental distractors, or thoughts that are irrelevant for the task at hand (i.e. task-unrelated thoughts or mind wandering). Although many of the findings reported in the Chapters 2-4 are in accordance with the executive-attention theory, others cannot not be explained in this rather simple framework (e.g. group differences on post-incongruent but not on post-congruent interference effects; large-scale connectivity patterns). Importantly, these findings do not contradict the theory, but rather, demonstrate that the relationship between individual's WMC and attention control abilities is more nuanced than previously suggested. These nuances emerged when combining several different research approaches: (1) analyzing entire distribution of responses, rather than comparing average performance; (2) tracking simultaneous allocation of attention to targets and distractors using novel paradigm; (3) measuring of localized brain activity, and interaction between brain networks.

As suggested by Kane and Engle (2003), specific task context reveals different aspects of WMC-related differences in attention control: Predominantly congruent trial context highlights differences in goal-maintenance, whereas predominantly incongruent trial contexts isolate differences in conflict resolution. In the Chapter 2 using RT distribution analyses, we found that WMC-related differences in interference resolution are more nuanced and can be detected only when a task is demanding enough to reveal differences in conflict resolution strategy. The importance of strategic differences related to variation in WMC was further highlighted in Chapter 3. Here, high- and low-WMC individuals used different strategies to minimize the effect of distracting information and to achieve similar behavioral performance. Finally, studies documented in Chapters 2 and 4 demonstrated that low-WMC is associated with a reactive style of conflict resolution and adjustment to the conflict, whereas high-WMC individuals tend to rely on a proactive control strategy. Interestingly, the relationship between WMC and trait impulsivity (as measured by BIS-11) in healthy subjects has been previously reported (Cools, Sheridan, Jacobs, & D'Esposito, 2007). In a

broader context, the findings presented in this thesis help to delineate the boundaries between variations in WMC and cognitive control abilities, and underscore the importance of using sensitive measures to detect such differences.

Before concluding, it would be remiss not to discuss unresolved issues and outline possible future directions. We found that there might be stable trait-like preferences for reactive or proactive control strategy in conflict resolution (Chapters 2 and 4), and different strategies to minimize distractor interference (Chapter 3). However, the utility of different strategies seems to be context-dependent (Chapter 2). Demonstrating effectiveness of one or the other strategy in different task contexts would be an important step to test an individual's flexibility in choosing particular strategy. Some evidence suggests that high-WMC individuals are more flexible in adopting different strategies depending on the task demands (Colflesh & Conway, 2007). Given that the relationship between WMC and cognitive control abilities are most often reported using the Stroop task (Table 1, Introduction section), it would be important to explore neural correlates of WMC-related differences in the Stroop task. In both EEG studies (Chapters 3 and 4) we used an extreme group design because we were interested in characterizing a specific dimension of individual differences and not estimating exact effect sizes. Although extreme-group design is statistically valid (Braver, Cole, & Yarkoni, 2010; Yarkoni & Braver, 2010), research presented in this thesis should be extended using continuous measures of WMC to characterize accurate effects sizes.

Several recent large-scale studies (Keye et al., 2013; Keye et al., 2009; Wilhelm et al., 2013) questioned predictions of the executive-attention theory of WMC, as no evidence was found to support the hypotheses of Kane and Engle (2003) of relationship between WMC and attention control abilities. These studies fall under the general concern of replicability and underpowered studies that is pervading many fields of science (Button et al., 2013; Pashler & Wagenmakers, 2012). The main solution to this problem is the suggestion to perform large-scale studies to increase statistical power (Button et al., 2013; Yarkoni & Braver, 2010). However, statistical power is directly related to the effect size and individual difference studies are by definition small-effect-size studies. Therefore, suggestions to formulate more specific and therefore testable theoretical predictions might be a more viable option for individual differences research (Chapter 5; Ashton, 2013). Without theoretical guidance, subtle but meaningful findings present in the data can end up labeled as "failed to replicate".

To conclude, results described in this thesis point to the need to update existing cognitive theories of WMC with neurophysiological findings from fMRI and EEG (Chapters 3 and 4; Cole et al., 2012; Faraco et al., 2011; Miller et al., 2012), as existing descriptive cognitive models are too under-specified to explain the richness and complexity of phenomena related to individual variations in WMC.

Nederlandse Samenvatting

Translated by
Barbara Nordhjem & Rene Passet

Werkgeheugen (WG) voorspelt ons vermogen om kennis te vergaren en nieuwe vaardigheden te leren (Pickering, 2006), en is een betere voorspeller van academisch succes dan IQ (Alloway & Alloway, 2010). Variaties in werkgeheugen zijn gerelateerd aan het leren van taal (Linck et al., 2013; Szmalec et al., 2012), leesbegrip (Daneman & Carpenter, 1980; Pimperton & Nation, 2012) en het oplossen van nieuwe problemen (Engle, Tuholski et al., 1999; Kane et al., 2004). Het is echter onduidelijk welke onderliggende neurobiologische mechanismen de variaties in het werkgeheugen tot stand brengen (Burgess et al., 2011).

Het identificeren van de neurologische mechanismes achter het werkgeheugen heeft belangrijke implicaties. Theoretisch gezien zou het een neuropsychologisch plausibele theorie kunnen opleveren waarin het mogelijk wordt om preciezere voorspellingen te kunnen doen (hoofdstuk 5). Praktisch gezien kan het leiden tot betere doelen tijdens trainingen en een betere evaluatie van het effect van training (Buschkuehl et al., 2012; Langer et al., 2013).

Het onderzoek zoals beschreven in deze thesis is gemotiveerd door een van de cognitieve theorieën van WG – de executive-aandacht theorie van WG (Engle & Kane, 2004; Kane et al., 2007; Kane & Engle, 2003). De theorie suggereert een nauwe relatie tussen individueel werkgeheugen en aandachtvermogen tijdens interferentie van gewone handelingspatronen, afleidende factoren an de omgeving, of gedachten die niet relevant zijn voor de bewuste taak (i.e. niet-taakgeralateerde gedachten of afwalende gedachten) zijn.

In deze thesis kijken we naar de vaak geziene relatie tussen werkgeheugen en prestatie tijdens respons-conflict taken (e.g., Simon taak, Eriksen flanker taak), die een uitdaging vormen voor iemands vermogen om taken uit te voeren terwijl ze worden afgeleid. Door de relatie tussen het WG en cognitief vermogen te karakteriseren zoeken we de verbreding van WG-onderzoek van het cognitieve tot het neurale niveau. Daarbij combineren we diverse analyses en experimentele benaderingen.

Het doel van de studie zoals gedocumenteerd in hoofdstuk 2 was om de vorespelling dat WG-gerelateerde verschillen in interferentie effecten zijn gekoppeld aan verschillen in de vaardigheid van conflictoplossing en niet alleen om de mogelijkheid om taakdoelstellingen te handhaven (Kane & Engle, 2003). Door het manipuleren van de moeilijkheidsgraad van *trial-by-trial* conflictoplossing in de Simon-taak en met gebruikmaking van reactietijddistributieanalyses, hebben we aangetoond dat er WG-gerelateerde verschillen zijn in het tijdsverloop van de verwerking van conflicten, in het bijzonder onder de moeilijke taakvoorwaarden. Onze hypothese was dat deze resultaten kunnen worden verklaard door het vermogen van hoog-werkgeheugenindividuen om een proactieve controlestrategie in te kunnen zetten als de behoefte aan controle hoog is, terwijl laag-werkgeheugenindividuen meer op een reactieve regelstrategie vertrouwen. Uit deze bevindingen bleek bovendien dat individuele verschillen in de snelheid van conflictoplossing contextafhankelijk zijn. Hoogwerkgeheugenindividuen zouden in staat kunnen zijn om een proactieve controlestrategie in te zetten en dus conflicten sneller op te lossen. De werkelijke gebruik van deze strategie is echter afhankelijk van de taakcontext.

De in hoofdstuk 3 beschreven studie werd uitgevoerd om de vraag of frequent waargenomen WG-gerelateerde verschillen in aandachtcontrole een afspiegeling zijn van de verschillen in het vermogen om taakirrelevante informatie te onderdrukken, of taakrelevante informatieve te vermeerderen. Hiertoe werd gebruik gemaakt van een nieuwe experimentele aanpak die het mogelijk maakte om de aandacht aan relevante en irrelevante informatie simultaan in een gewijzigde Eriksen flankertaak met EEG *frequency tagging*-techniek te

meten. De resultaten van deze studie tonen aan dat hoge en lage WG-mensen verschillende strategieën gebruiken om vergelijkbare prestaties te bereiken: Hoogwerkgeheugenindividuen zijn gericht op het onderdrukken van irrelevante informatie, terwijl laagwerkgeheugenindividuen zich richten op het vermeerderen van relevante informatie.

De studie beschreven in hoofdstuk 4 is gericht op manieren waarop grootschalig netwerkfunctioneren zoals gemeten met EEG verschillen tussen hoog-en laag-werkgeheugenindividuen tijdens de verwerking en aanpassing aan conflict kan karakteriseren. Uit de bevindingen van deze studie bleek dat, hoewel hoog- en laag-werkgeheugenindividuen niet gedragsmatig verschillen, er grote WG-gerelateerde verschillen bestonden in de theta-(4-8 Hz) en delta-band (1-3 Hz) connectiviteit in het frontopariëtale netwerk. Deze bevindingen suggereren een verklaring voor de zwakke relatie tussen het WG en gedragprestaties in interferentietaken. Ook wordt duidelijk dat WG-gerelateerde verschillen in cognitieve controle subtieler zijn dan de executive-aandacht theorie voorspelt, en dat maatregelen gevoeliger dan reactietijd en foutenpercentages nodig zijn om deze relatie te ontdekken.

Veel van de bevindingen gerapporteerd in de hoofdstukken 2-4 zijn in overeenstemming met de executive -aandacht theorie van het WG, maar anderen kunnen niet worden verklaard in dit vrij eenvoudige theoretische kader (bv. groepverschillen op post-incongruent maar niet op post-congruent interferentieeffecten; grootschalige connectiviteitpatronen). Belangrijk is dat deze bevindingen niet in tegenspraak zijn met de theorie, maar eerder aantonen dat de relatie tussen de WG en aandachtcontrolecapaciteiten van het individu genuanceerder is dan eerder gesuggereerd.

Tot slot, de resultaten zoals in dit proefschrift beschreven, wijzen op de noodzaak om de bestaande cognitieve theorieën van het WG te vernieuwen met neurofysiologische bevindingen uit fMRI en EEG onderzoek (hoofdstuk 3 en 4; Cole et al., 2012; Faraco et al., 2011; Miller et al., 2012), omdat bestaande beschrijvende cognitieve modellen tekort schieten om de rijkdom en complexiteit van de verschijnselen in combinatie met individuele variaties in het WG (hoofdstuk 5) te verklaren.

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Gulbinaite, R., Johnson, A. (2013) Working memory capacity predicts conflict-task performance. Quarterly Journal of Experimental Psychology 67(7), 1383-1400.

Submitted manuscripts

Gulbinaite, R., Van Rijn, H., Cohen, M.X . Fronto-parietal network oscillations reveal relationship between working memory capacity and cognitive control

Book chapter

Johnson, A., Gulbinaite, R. (2012). Performance Monitoring and Error-related Brain Activity. In Neuroergonomics: A Cognitive Neuroscience Approach to Human Factors and Ergonomics (Johnson, A. & Proctor, R.W. Ed.)

Biography

Rasa Gulbinaite was born “on the paper” in Kaunas (practically in Klaipeda maternity home) and grew up in Vilnius (Lithuania). In 2001 she started her training as a medical doctor. However, soon it was clear that biochemistry and physics were much more interesting than internal medicine. In 2003 she decided to pursue an academic career and in 2007 she was granted a Bachelor degree in Biophysics. She continued her training in Vilnius University and earned a Master’s degree in Neurobiology. At the same time she worked as a project manager in an international market research company. This slight detour of having a “real” job albeit challenging and enriching (data analysis, project management, focus group discussions, and presentations) made it clear that scientific career should be given a chance.

In the winter of 2009 she arrived to Groningen to start a PhD project. Under supervision of Addie Johnson and Hedderik van Rijn she completed the current thesis on neural mechanisms underlying individual differences in working memory capacity. Using EEG as a primary tool she provided neural evidence for the proposed relationship between individual differences in working memory capacity and attentional control.

In October, 2014 she will start a post-doc in the lab of Rufin VanRullen (Centre de Recherche Cerveau et Cognition, Toulouse, France) studying the role of brain oscillations on visual perception.